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Original Article

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Running title: Use of harsh environments across a phylogeny

Word count (Abstract - references, included): 8446 words

Printed page estimation: title/abstract etc.: 1 page, Introdcution – Discussion : 5956 words ≅ 6 pages, 94 refernces ≅ 3 pages, tables and figures: 1.5 pages (table 1 could be shifted to Appendix)

Estimate of number of journal pages required by table and figures: 1.5 (Tab. 1 could also be moved to an Appendix if needed)

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ABSTRACT

Aim Certain species have few living relatives, i.e., occupy low clade ranks. Hence, they possess high conservation value and scientific interest as unique representatives of ancient lineages. However, we do not know whether particular environments favour the maintenance of low clade ranks or whether the distribution of environments across the globe affects the global distribution of clade ranks and, hence evolutionary uniqueness. In this study, we tested whether and how harsh environments decrease the clade ranks of the species that inhabit them.

Location Global

Methods We described the phylogeny of the collembolan genus *Willemia* by a parsimonious method based on 52 morphological characters and estimated the species' use of harsh environments (polar, high-mountain, desert, polluted, waterlogged, saline, and acidic) from 248 publications.

Results We found that the use of different types of harsh environments is maintained among close relatives and has similar phylogenetic signals (except for the use of salinity). The use of harsh environments might therefore affect the diversification of lineages. Correcting for the phylogenetic non-independence of species, we found that species using harsh environments have comparatively low clade ranks. We also found that species using harsh environments occur almost exclusively on former Laurasian continents and that as a statistical consequence, Laurasian species tend to have lower clade ranks.

Main Conclusions We suggest that harsh environments maintain low-clade-rank species by decreasing, simultaneoulsy or successively, extinction and speciation, which may eventually explain the major variation in clade rank across the globe.

Keywords abiotic stress; diversification; habitat; niche conservatism; phylogenetic reconstruction; phylogenetic generalised least squares; phylogenetic principal components; phylogenetic permutation; root-skewness test; tropical

INTRODUCTION

Extant species can occupy very different clade ranks within a phylogenetic topology. Certain species have very few living relatives and thus occupy a low clade rank, whereas others have much higher clade ranks. Species of low clade rank are the sole extant representatives of their lineages and hence have a high evolutionary uniqueness: the loss of a low-clade-rank species implies the loss of more evolutionary history than the loss of a high-clade-rank species (Purvis *et al.*, 2000; Prinzing *et al.*, 2004; Colles *et al.*, 2009). For this reason, it is important to understand whether low-clade-rank species are maintained to a greater extent in certain environments or regions than in others.

It has been suggested that species of low clade rank persist and accumulate in regions with low extinction rates (Willis, 1922; Condamine *et al.*, 2012), notably due to relatively stable climates, especially in the tropics (Wiens & Donoghue, 2004; Jablonski *et al.*, 2006; Hawkins *et al.*, 2007; Donoghue, 2008; Buckley *et al.*, 2010). Furthermore, low clade rank has been suggested to reflect a relatively low speciation rate, as has been proposed for the regions outside the tropics (Willis, 1922; Jablonski, 1993, 1999; Chown & Gaston, 2000; Jablonski *et al.*, 2006). Overall, species of low clade rank can be expected to most likely accumulate in regions in which a low speciation (or immigration) rate very roughly outweighs a low rate of extinction (or emigration). There would be no net effect on species richness under such circumstances.

The distribution of clade ranks across regions has received considerable attention, whereas the distribution of clade ranks across types of environments (broadly, “habitats”) has received much less attention. Bartish *et al.* (2010) have recently shown that within a region, particular harsh environments might be colonised by species of particularly low clade rank: across 40 different habitats in the Netherlands, those with extremely high soil moisture and

extremely low soil pH were characterised by low mean clade ranks of their angiosperm inhabitants. However, this analysis was restricted to a single, small region and might not reflect (or influence) globally coherent patterns. Here, we define abiotically harsh environments as environments that tend to impose a major direct physiological stress on most species of a given lineage — i.e., a constraint on growth and reproduction (sensu Grime, 1977) — with the obvious exceptions of highly tolerant species and sub-lineages. We can speculate that harsh environments might indeed reduce extinction rates, as patches of harsh environments remain present at least locally at any given time in any region and maintain gene flow (Behrensmeyer et al. 1992), and species in harsh environments might rarely be driven to extinction by biotic interactions (Grime 1977, Callaway et al. 2002). In addition, harsh environments might possibly reduce speciation rates by reducing two of the major triggers of speciation: (i) recombination events, which become rarer with environmental harshness due to increased generation times (Grime 1977), and (ii) evolutionary arms races between prey and their natural enemies, which become less diverse with harshness due to a reduction in the number of trophic levels (Vermeij 1987). We therefore hypothesise that clade ranks are lower in harsh environments (whereas species richness is not affected).

Whatever the relationship between environmental harshness and clade rank, the existence of such a relationship requires that there is no trade-off between the capacity to use different types of harsh habitats; otherwise, the average harshness of the habitat used by any species would be intermediate (see Hoffmann & Parsons, 1997 for possible mechanisms). The existence of a relationship between harshness and clade rank would also require that the use of harsh and mesic environments is phylogenetically conserved so that related species tend to have similar affinities to harsh and mesic environments (see Prinzing *et al.*, 2001, phylogenetic signal sensu Losos, 2008). Without such conservatism, past patterns of speciation and extinction in ancestral environments would not be transmitted to distributions

of clade ranks in present-day environments (Condamine *et al.*, 2012). However, certain authors suggest that the capacity to use harsh environments can evolve and disappear rapidly (see Hoffmann & Parsons, 1997 and Hoffmann & Willi, 2008 for mechanisms), particularly if expansions and constrictions of such harsh environments may trigger the acquisition or loss of the capacity to use these environments (Gaston, 1998) and if the use of harsh environments imposes a cost (but see Gaston, 2003).We hence hypothesise that the use of harsh habitats is not constrained by a trade-off between different types of harshness and is phylogenetically conserved.

Should particular environments maintain low-clade-rank species and particular regions maintain these particular environments and their inhabitants, we would expect to observe that these regions also maintain many low-clade-rank species (see also Donoghue, 2008). We can speculate that selection might have favoured the use of harsh habitats far from the tropics (Jablonski, 2008), especially in the Northern Hemisphere, where a steep latitudinal gradient of decreasing biodiversity can be observed today (Chown *et al.*, 2004). Given that the clade rank of a species reflects the outcome of millions of years of evolutionary history, the past differentiation of regions, notably the distinction between Laurasia and Gondwana, might be more important than their present-day configuration. One might speculate that past environments were harsher, on average, in Laurasia than in Gondwana (Vršanský, 2005; Crisp *et al.*, 2010), reflecting, among other differences, the larger surface area of the landmasses in northern compared to southern temperate regions. Larger landmass would produce more climatic and thereby edaphic extremes in Laurasia and its descendent land masses than in Gondwana, except for Antarctica (Chown *et al.*, 2004). Additionally, even restricted periods of harsh conditions might leave a strong signal in a continental fauna if the vast majority of the continent became harsh and later recolonisation was slow. This regional origin and maintenance of species might still be reflected by a larger number of low-clade-rank species

in landmasses stemming from Laurasia (centres of origin, Myers & Giller, 1988). Moreover, independent of the above speculations, given what we know of the present worldwide distribution of soils (FAO-UNESCO, 2007), climates (World Climate Map, 2012) and human activities, harsh environments (e.g., soil acidity, drought, frost, waterlogging, heavy metal contamination), with the exception of seashore salinity, appear to be more widely distributed in ex-Laurasian than in ex-Gondwanan continents. Whatever the precise causes, we can hypothesise that non-tropical regions and those of Laurasian origin harbour more low-clade-rank species, largely as a consequence of the increased numbers of species using harsh habitats.

The predictions derived from these hypotheses can be tested across extant species belonging to monophyletic lineages that are ancient (having survived several ecological crises and dating back to the Laurasia/Gondwana epochs), highly diversified and distributed worldwide. Collembola (springtails) are one such old, diversified lineage dating back to the Early Devonian (Hirst & Maulik, 1926; Greenslade & Whalley, 1986; Grimaldi, 2010), and most actual forms, at the family or even genus level, are known from the Cretaceous (Christiansen & Pyke, 2002a, b). Among the cladistic studies conducted on Collembola, the genus *Willemia* deserves special attention given its wide distribution from both an ecological and a biogeographical point of view. The genus is monophyletic and comprises a large number of species for which phylogenetic trees can be reconstructed unambiguously (D'Haese & Weiner, 1998; D'Haese, 1998, 2000 for subtrees of the genus). In addition, certain species of *Willemia* are known for their preferential use of arid (Thibaud & Massoud, 1988), polar (Sørensen *et al.*, 2006), mountainous (Loranger *et al.*, 2001), acidic (Ponge, 1993), saline (D'Haese, 2000), or polluted (Filser & Hölscher, 1997) environments. The genus is also representative of many others in the absence of a time-calibrated phylogeny due to the scarcity of fossil records. This lack of information renders approaches based on branch

length inapplicable but does not affect approaches based on clade ranks. Obviously, *Willemia* is only one out of an almost infinite number of genera. However, studying one genus may help to develop a methodological approach for teasing apart the associations between the use of harsh environments and patterns of diversification within a phylogenetic context. This approach may then be applicable to other genera and larger taxonomic units.

To evaluate the relationship between the use of harsh environments and clade rank, we tested whether (i) the use of different types of harsh environment is positively rather than negatively correlated (i.e., species tend to be able to tolerate either a broad range of harsh environments or none) and is phylogenetically conserved in the sense of being more similar among phylogenetically closely related species than among more distantly related species; and (ii) species using harsh habitats consistently occupy low clade ranks rather than being randomly scattered across the phylogeny, and these harsh environments tend to be the ancestral environments of such low-clade-rank species, which are as numerous as species absent from such harsh environments. To evaluate the relationship between geographic region, use of harsh environments and clade rank, we tested whether species outside the tropics occupy lower clade ranks than species within the tropics, due to a tendency of non-tropical species to use harsher habitats. We also tested whether species on former Laurasian land masses occupy lower clade ranks than species on former Gondwanan land masses, due to a tendency to use harsher habitats. In all analyses we accounted for the statistical non-independence of species. We also conducted character mapping to reconstruct ancestral stages and explore whether the environments and regions used by species are indeed ancestral to the respective (sub)lineage and hence might have influenced the clade rank of the respective species in that (sub)lineage.

MATERIALS AND METHODS

The genus *Willemia* and the reconstruction of its phylogeny

Within the Class Collembola, the genus *Willemia* belongs to the Hypogastruridae family. It differs from other hypogastrurid genera by the total lack of pigment or furcula and the small size of the slender body, which never exceeds 1 mm in length (Thibaud, 2004). According to their life form, all *Willemia* species belong to the euedaphobiont sub-category Bc3b (small size, slender body, no furcula) of Rusek (2007). The study addresses 42 of the 43 species currently known worldwide in this genus (list in Appendix S1b). The absent species was only described in 2011 by D'Haese & Thibaud, so its environmental or geographic distribution is still very far from being sufficiently documented. The genus is distributed worldwide, with 15 species recorded only in the tropics, 25 species outside the tropics and only 2 species present both in the tropics and elsewhere (details about the biogeographic distribution of species in Appendix S2e). A total of 13 species were recorded from continents and islands of Gondwanan origin vs. 20 of Laurasian origin and 9 of uncertain origin (Appendix S2e). As for most Collembola, dispersal modes are still unknown, although sea currents have been suspected to favour long-distance transport (Thibaud, 2007). *Willemia* species live in the soil (from litter to mineral soil, whether acid or alkaline), in psammic environments (beaches, sand dunes, deserts) and in caves, but not all of them are found in harsh environments (Table 1). Overall, the great variation in the biogeographic and ecological distributions of species, together with a sufficient but still-manageable number of species, makes this genus a good model for testing hypotheses about relationships between biogeography, ecology and the evolution of extant species.

The reconstruction of the phylogeny of the genus *Willemia* is explained in Appendix S1a-d. This reconstruction confirmed the monophyly of the genus already established by

D'Haese (2000). We were constrained to use morphological characters, as explained and justified in Appendix S1a. Obviously, speciation may not always leave morphological traces, and such "cryptic" speciation is overlooked if morphological characters alone are considered. This outcome is especially probable in lineages with morphological characters that are few in number or unstable in terms of shape and/or position (among Collembola, e.g., genera *Folsomia* and *Parisotoma*). *Willemia*, however, has numerous characteristics (e.g., hairs, sensilla, vesicles) of stable shape and position. Due to this feature of the genus, speciation is unlikely to be cryptic in *Willemia*. Cryptic speciation may be more frequent at the population level, but such ephemeral population phenomena were not of interest in our study. We also note that a dated phylogeny is not feasible for *Willemia* given the lack of dating points caused by the absence of fossils for this genus.

All analyses were run on each of the 6 most parcimonious phylogenetic trees as well as on a strict-consensus of 6 phylogenetic trees (detailed in Appendix S1: Phylogenetic reconstruction). The results from analyses run on the strict consensus tree are given in te Results section, those from the 6 indiviudal trees in the corresponding appendices (detailed in Appendix S3: Reconstruction of ancestral states)

Use of harsh environments and the biogeographic distribution of *Willemia* species

The use of harsh environments (as defined in the Introduction) was indicated by the occurrence of *Willemia* species in environments known for at least one factor that is thought to be a major constraint for most soil-dwelling organisms (see Hopkin, 1997 for springtails): i.e., xeric, hydric, arctic, alpine, acidic, metallic or saline soils. See Appendix S2a for detailed definitions of these factors and literature research methods and Appendix S2b for references. A 'harshness breadth' index was estimated for every species based on the number of harsh

environments in which the species was recorded, scaled from 0 (no harsh environments recorded for the species) to 7 (all harsh environments recorded).

Biogeographic distributions were categorised as (*i*) tropical (between the tropic latitudes, Inter-Tropical Convergence Zone, ITCZ) or non-tropical (north or south of the tropic latitudes) and as (*ii*) Gondwanan or Laurasian following the maps by Christiansen & Bellinger (1995), as detailed in Appendix S2e. Appendix S2e also outlines the relationships between tropical/non-tropical and Laurasia/Gondwana classifications and between regions and harshness.

Statistical Analyses

The correlation among uses of different types of harsh environments across lineages was analysed by a phylogenetic Principal components analysis (pPCA), a multivariate method recently devised by Jombart *et al.* (2010b) by extending a methodology developed in spatial ecology and spatial genetics to the analysis of phylogenetic structures in biological features of taxa.

Phylogenetic conservatism is the tendency of closely related species to share similar values for a given trait (typically more similar than distantly related species, Wiens *et al.*, 2010). We predicted phylogenetic conservation of the use of harsh environments, i.e., that related species tend to have similar harshness breadth index values. Here, harshness breadth varied from 0 to 7 harsh environments as defined above. Phylogenetic conservatism for harshness breadth was tested with the Pavoine *et al.* (2010) approach. Briefly, the total trait diversity of the lineage was decomposed across the nodes of a phylogenetic tree by attributing to each node a value measuring the differences among lineages descending from that node weighted by the proportion of species descending from it. Permutation tests (999 replicates)

allowed the attribution of a probability to the observed value. Our principal test was the root-skewness test, which verifies whether phylogenetic distances between species correspond to distances in a given trait. Supplementary tests in Pavoine *et al.* (2010) explore whether trait variation is concentrated on a single node or on a few nodes, but that work cannot be presented in detail here (usually, the former were not significant, whereas the latter were). Phylogenetic distances were measured as nodal distances, i.e., the number of nodes on the shortest path that connects two species on the phylogenetic tree. For measuring distances between species in terms of habitat harshness (a multi-choice variable), we used the simple matching coefficient (Sokal & Michener, 1958): (a+b)/(a+b+c+d), where 'a' is the number of harshness types in common, 'b' is the number of harshness types with which neither of the species are associated, and 'c' and 'd' are the numbers of harshness types unique to each of the two species.

Losos (2008) has suggested that the term 'phylogenetic conservatism' should only be used if trait change along the phylogeny is slower than Brownian motion and that the term 'phylogenetic signal' should be used for the wider phenomenon of correlations between trait distance and phylogenetic distance. However, properly identifying the rate of trait change would require a dated phylogeny, which is not feasible for Collembola. Moreover, whereas change in the use of harsh environments may be considered 'random' and not 'conservative' from the point of view of phylogenetic reconstruction, it is still much more 'conservative' than the changes in the harshness of the environment surrounding the animals. For simplicity, we therefore retain the term 'conservatism' and use it in the sense of a pattern, not of a process (see Wiens *et al.*, 2010 for further discussion on phylogenetic conservatism).

We then tested the link between harshness breadth as a response variable and (*i*) phylogenetic clade rank, (*ii*) tropical/non-tropical classification and (*iii*) Gondwana/Laurasia classification as explanatory variables. Any test of hypotheses on the environmental and

277 geographic correlates of clade ranks of species is vulnerable to the phylogenetic non-
278 independence of species. A classical approach to the problem of phylogenetic non-
279 independence is the use of sister-clade comparisons (Felsenstein, 1985), but this approach is
280 not applicable in our case because sister clades have the same clade ranks by definition. An
281 alternative and more general approach is to include co-matrices of phylogenetic proximity in a
282 phylogenetic generalised least square fit (PGLS) as described in Martins & Hansen (1997),
283 using the method of Grafen (1989) to estimate branch lengths. To increase the symmetry of
284 the harshness breadth distribution, this variable was square-root transformed.

285 We tested the relationships between the phylogenetic clade ranks of species as the
286 dependent variable and either the species' tropical/non-tropical classification or their
287 Gondwana/Laurasia classification as the independent variable. We conducted alternative
288 analyses, either incorporating the uses of harsh habitats as covariables or not incorporating
289 these uses. As the dependent variable was directly inferred from the species' phylogenetic
290 position and was, thus, a characteristic of the phylogeny, we incorporated phylogenetic non-
291 independence in the explanatory variables as follows. We computed the F-statistic associated
292 with each variable using an ordinary linear model. We then estimated a theoretical
293 distribution of this statistic via the method of phylogenetic permutation described by Lapointe
294 & Garland (2001, see also Harmon & Glor, 2010): closely related species are more likely to
295 exchange values than more distantly related species. The values of the explanatory variables
296 were permuted (999 times) by this approach, keeping the phylogenetic clade rank unchanged.
297 The P-value was then calculated as the proportion of theoretical values of the F-statistic that
298 were higher than or equal to the observed value. We note that species that occurred in both the
299 Laurasia and Gondwana biogeographic domains (6 species) or were on continents or islands
300 of uncertain origin (3 species) and species that were recorded both within and outside the
301 tropics (2 species) were discarded from geographic analyses.

All these methods were implemented in R (R Development Core Team, 2010), which was used for all statistical calculations. The packages used were ade4 (Dray & Dufour, 2007), adephylo (Jombart *et al.*, 2010a), ape (Paradis *et al.*, 2004), and nlme (Pinheiro *et al.*, 2010). The R codes are available upon request.

For character mapping, we used Mesquite (Maddison & Maddison, 2011); specifically, we used parsimony and stochastic character mapping. As both approaches produced the same results, we only present the parsimony mapping, which suffers less from the absence of biogeographic classifications for individual species.

RESULTS

The characters and phylogeny of *Willemia* are provided in Appendix S1b and Appendix S1d, respectively. Note that there is no phylogenetic structure in the study intensity of *Willemia* species (i.e., the numbers of references), and hence, the analyses presented below are not biased by study intensity (Appendix S2c). Although branch lengths are not available, as explained in the Introduction, there is a major variation in the clade rank of species, ranging from 2 to 13, reflecting substantial variation in the number of extant close relatives across species.

Uses of most types of harsh habitats are positively correlated

The phylogenetic principal components analysis (pPCA) indicated strong positive correlations between all types of harsh habitats with the exception of salinity. The use of all other types of harsh habitats showed clear positive scores on the same principal component axis (Fig. 1). A visual examination of Table 1 (where species are arranged according to their order in the phylogenetic tree) confirms this result: with the exception of salinity, the use of all types of harsh habitats appears to be phylogenetically positively correlated. Given that the use of saline habitats corresponded to the absence of all of the other six types of harsh habitats, we excluded salinity from further analyses to better capture the overall syndrome of harsh habitat use (see also Appendix S2d).

Phylogenetic conservatism in the use of harsh habitats

The types of harshness under which species were found exhibited clear phylogenetic conservatism (root-skewness test P=0.002). Additionally, the number of types of harsh

habitats used by a species (harshness breadth) was phylogenetically conserved (root-skewness test; P=0.042). If salinity was excluded from the array of harsh habitats (given that it is not positively related to other harshness factors, see above), a stronger conservatism of harshness breadth was found (root-skewness test P=0.013). The presence/absence of *Willemia* species in harsh habitats (rather than the number of harsh habitats used) exhibited an even clearer phylogenetic conservatism if salinity was excluded from the array of harsh habitats (root-skewness test P=0.001). This phylogenetic structure was confirmed using parsimony character state reconstruction (Fig. 2 a). These results are based on the consensus tree but are robust to phylogenetic uncertainty and were found in all 6 of the equally parsimonious trees (Appendix S3).

Species using harsh habitats have lower clade ranks but are as numerous as species using mesic habitats

We found that the clade rank of a species decreased with the species' harshness breadth (PGLS; P=0.002). If salinity was excluded, it appeared that the distance to the root of the phylogenetic tree was quite similar for all species using harsh habitats independently of the number of harsh habitat types they were using, with all harshness-tolerant species occupying a basal position (Fig. 3). The ancestral nature of life in harsh habitats was also visually assessed through parsimony character state reconstruction (Fig. 1 a), mapping the use of harsh habitats (salinity excluded) and other habitats on the cladogram. Most of the 22 harshness-tolerant species were located close to the root, i.e., they corresponded to a "basal" pool of species including all species from *W. multilobata* to *W. denisi* in Fig. 1 a. Only three species in this group did not confirm that harshness tolerance was an ancestral character: *W. bellingeri*, *W. psammophila* and *W. unispina*. Species belonging to the most advanced group, in contrast,

were not found in harsh habitats (except for saline habitats) with the exception of *W. nepalensis*. All these results are based on the consensus tree but are robust to phylogenetic uncertainty and were found in all 6 of the equally parsimonious trees (Appendix S3).

In total, there were 22 species using harsh habitats and 20 species using only mesic habitats (i.e., species that were never recorded in any of the harsh habitat types considered except salinity). This result is not significantly different from equality (df=1; Chi^2=0.095; P=0.758).

Geographical distribution: species using harsh habitats tend to be Laurasian, and as a statistical consequence, Laurasians tend to have low clade ranks

We found that species using harsh and mesic habitats were distributed differently across the globe. Species using harsh habitats tended to occur in non-tropical regions, although the relationship was relatively weak (Fig. 4a; PGLS; df=30; t=2.29; P=0.029). At the same time, species using harsh habitats were strongly restricted to regions of Laurasian origin (Fig. 4b; PGLS; df=30; t=3.19; P=0.003). In fact, only two harshness-tolerant species were recorded outside former Laurasia (*W. trilobata* and *W. namibiae,* Appendix S2e). These results are based on the consensus tree but are robust to phylogenetic uncertainty and were found in all 6 of the equally parsimonious trees (Appendix S3).

Low-clade-rank species were strongly restricted to present non-tropical regions (Fig. 5a; n=31 as in all tests of this paragraph, tests based on phylogenetic permutations, F=26.14: P=0.001, and see character state reconstruction, Fig. 1b). This relationship was maintained if harshness breadth was included as a co-variable: harshness breadth and presence in present-day non-tropical regions were both related to low clade rank (F=23.90; P=0.001 for harshness breadth, and F=9.76; P=0.007 for presence in present-day non-tropical regions; conclusions

were not impacted by the order in which the two explanatory variables were entered in the model; harhness first: F=29.17; P=0.001, harshness second: F=4.48; P=0.048). Therefore, the high harshness tolerance of non-tropical species did not explain their low clade rank. Species of low clade rank also tended to be restricted to former Laurasia regions (Fig. 5b; F=10.47; P=0.006 and see character state reconstruction, Fig. 1c). If occurrence in former Laurasia was included first in the model and harshness breadth second, both variables were significant (F=12.68; P=0.002 for occurrence in former Laurasia and F=7.33; P=0.014 for harshness breadth). However, this relationship disappeared if harshness breadth was added to the model first: in this case, occurrence in former Laurasia was no longer significant (F=1.31; P=0.262), whereas harshness breadth was still significantly related to low clade rank (F=18.69; P=0.001). Overall, this result indicates that species using harsh environments are particularly bound to former Laurasia continents (above paragraph) and that — as a statistical consequence — we find many species of low clade rank on former Laurasia continents. All these results are based on the consensus tree but are robust to phylogenetic uncertainty and were found in all 6 of the equally parsimonious trees (Appendix S3).

DISCUSSION

We found that uses of different types of harsh environments are maintained among close relatives and have similar phylogenetic signals with the exception of use of saline habitats. Use of saline habitats is thus not consistent with our hypotheses (see Introduction) and was excluded from further analyses. There are two opposing lines of explanation for this exception. First, one can argue that tolerance of saline conditions comes with a major cost in terms of tolerance of multiple other harshness factors, and thus, salinity tolerance will not increase the overall capacity to use harsh environments and will be lost rapidly through

evolution if no longer needed. Second, there are putative arguments suggesting that salinity is not a form of harshness from the point of view of Collembola (Appendix S2d). Pending more ecophysiological studies on the tolerance of springtails to sea water, it might be suggested that life in contact with dilute saline solutions (seashores but not dry saline environments) requires no special adaptation in basal Hexapoda, in contrast to fully terrestrial insects (higher insects).

Using a phylogenetic framework, we showed that among *Willemia* springtail species, the use of harsh habitats (tolerance of harshness) displayed a strong pattern of phylogenetic conservatism and no phylogenetic trade-off in the capacity to use different types of harsh habitat (except for salinity, see Appendix S2d). These results ultimately suggest that the use of harsh habitats can affect the mode of diversification of these lineages and, thereby, the distribution of clade ranks across habitats and eventually regions. In fact, we found that species using harsh habitats have significantly lower clade ranks.

Although the occurrence of archaic life forms has already been documented in specific exotic and harsh habitats such as volcanoes, hot springs, deserts and ice caps (Oliver *et al.*, 2000; Nriagu, 2003; Labandeira, 2005; Oliver *et al.*, 2005; Ehrhardt *et al.*, 2007), a systematic link between species clade rank and habitat harshness has not, to our knowledge, been demonstrated previously. Lower clade ranks would be consistent with lower speciation rates in harsh habitats. However, we also found that species using harsh habitats are even slightly more numerous than species using mesic habitats. This combination of results is consistent with a scenario of decreased net extinction of species combined with decreased net speciation in harsh habitats. We stress, however, that we can only speculate on speciation and extinction averaged across time; we do not know whether this pattern reflects permanently low speciation rates combined with permanently low extinction rates or, for instance, initially high speciation and very low extinction rates combined with later very low speciation rates combined with high extinction rates. Both scenarios may produce the same low clade ranks of

extant species. Independently of the precise mechanisms, harsh habitats function today as museums of low-clade-rank species, i.e., of species that are the last extant representatives of ancient lineages.

Such a pattern of conservatism and of the preferential presence of low-clade-rank species in harsh habitats may ultimately result in the global distribution of harsh-habitat species driving the global distribution of low-clade-rank species, as predicted. In fact, we found that species using harsh habitats exhibit distinct geographic distributions — they are more numerous outside the tropics and, in particular, on former Laurasia — and that species of low clade rank match these distributions. In addition, for Laurasia, the occurrence of low-clade-rank species is, in fact, explained by the occurrence of species in harsh habitats. For this reason, the geographically conserved use of harsh habitats decreases the phylogenetic clade rank of species on the continents of former Laurasia.

Our results contribute to the debate on the evolutionary fate of 'generalists' versus 'specialists'. Generalists are thought to be better able to overcome ecological crises (Raup, 1986; Zhou *et al.*, 2005). More recently, however, Colles *et al.* (2009) showed that different phylogenetic approaches may lead to diverging conclusions. Our present phylogenetic study compares 'harshness generalists' to species putatively specialising in habitats lacking any of the harshness factors. The results are consistent with a longer survival of 'harshness generalists' and hence rather point towards generalists being, in fact, less susceptible to environmental change than specialists. However, our study also indicates that reduced extinction might possibly be coupled with reduced speciation, as this has been shown with other traits, e.g. geographic range (Parker *et al.*, 1999), leaving practically no net effect on the numbers of species using harsh habitats.

Our results point to a common factor of tolerance of environmental harshness, which would be shared by a pool of low-clade-rank species, as uses of different harsh habitats were positively correlated with one another. This result is not surprising in view of the roles of soil acidity, altitude and latitude: the biologically active part of the soil (the topsoil) becomes more acidic as the decomposition rate of organic matter decreases, leaving the organic matter humified rather than mineralised (Ulrich, 1986; Ponge, 2003, 2012). However, it was more surprising to find relationships between these three factors and drought or metallic pollution. The only point in common among these five factors appears to be a decrease in biological activity caused by harsh environmental conditions. To explain these positive relationships among different types of harshness tolerance, we should first examine the cellular level. The integrity of cell membranes, combined with active cellular repair, is known to protect a wide array of organisms from death caused by environmental hazards (Nriagu, 2003; Oliver *et al.*, 2005; Shi *et al.*, 2008; Timmermans *et al.*, 2009). This feature could be the most primitive mechanism of harshness tolerance, requiring no specialised adaptation to any particular harshness factor but rather the coordinated expression of genes functioning in common in a 'general-purpose genotype' (Weider, 1993; Niehrs & Pollet, 1999; Vohradsky *et al.*, 2000; Van Doninck *et al.*, 2002; Kaplan *et al.*, 2004). For instance, it has been shown that drought acclimation produces cold tolerance in springtails (Holmstrup *et al.*, 2002) and that long-chain fatty acids of phospholipidic membranes are involved in this phenomenon (Bayley *et al.*, 2001). These findings are consistent with the evolutionary importance of membrane integrity (Jobson *et al.*, 2010). Adaptation to harsh environments may occur rapidly if a phylogenetic lineage already possesses an efficient array of regulatory genes, known to be as evolutionarily important as changes in enzyme structures (Roelofs *et al.*, 2006, 2010). However, the evolutionary acquisition of this gene array might be difficult and might only occur rarely. This

hypothesis is consistent with our observation of only a few cases of independent acquisitions of the capacity to use harsh habitats.

We showed that derived species of high clade rank were primarily tropical species (while not all tropical species are derived), an observation also made for marine bivalves by Harnik et al. (2010). This result is in contrast to the tropical conservatism hypothesis of Wiens & Donoghue (2004), which suggests that the tropics, representing supposedly more ancient environments, should harbour more ancient species characterised by low clade ranks (without excluding more recent species). Our results could be explained by a more ancient origin of environments observed today outside of the tropics, compared to today's tropical environments (Smith *et al.*, 2007). However, across the lifetime of the Collembola lineage, the tropical environments are usually considered to be at least as old as the non-tropical ones (e.g., Behrensmeyer *et al.*, 1992). Alternatively, our results can be explained if the low clade rank of species results from a trait such as the capacity to use harsh habitats and if species with this trait tend to occur outside rather than inside the tropics. However, we found that the tropical/clade-rank relationship was independent of the use of harsh habitats. The observed high clade ranks of tropical species therefore remain unexplained. Potentially, traits other than the use of harsh habitats need to be considered, as well as an interplay between environmental filters (mainly operating out of the tropics) and evolutionary potential of lineages (mainly operating in the tropics), as postulated by Harnik et al. (2010). We note, however, that most tropical species are found on territories of Gondwanan origin and that the high clade rank of Gondwanan species, in turn, could be explained by their present-day use of mesic habitats. Our results may thus point to a link between niche conservatism, diversification, and biogeographic distribution leading to patterns that are inconsistent with those predicted by Wiens & Donoghue's (2004) tropical conservatism hypothesis. It remains to be tested whether

503 the patterns we observed are a rare exception for a small group of species or can be found
504 more frequently, e.g., in other groups of invertebrates.

505 By creating harsh environments (acid rain, polluted water, soil and atmosphere,
506 vegetation-less areas) throughout the world and by accelerating species dispersal (alien
507 introductions), humans select for particular major lineages to the detriment of others (Purvis,
508 2008; Ozinga *et al.*, 2009; May, 2010). However, our results show that by rendering global
509 environments increasingly harsh, humans also select for particular evolutionary scenarios to
510 the detriment of others: increasingly abundant harsh environments appear to represent
511 museum scenarios, i.e., environments that accumulate low-clade-rank species. It is possible
512 that this outcome is due to low extinction and speciation rates. In contrast, environments of
513 low harshness become rare and therefore potentially represent a cradle scenario, i.e.,
514 environments that accumulate high clade-rank species, due perhaps to high rates of speciation.
515 Another result is that the use of harsh habitats is apparently a character that, in most cases,
516 does not originate de novo when needed but is carried by particular species for very long
517 periods of time. A high priority should thus be given to the conservation of this pool of low-
518 clade-rank species. However, other studies are necessary to ascertain the generality of the
519 patterns we discerned in one ancient animal group, Collembola. These studies should focus on
520 other ancient but highly diversified groups, such as mites and mosses, which are suspected to
521 be relatively tolerant of harsh environments (Prinzing *et al.*, 2000; Oliver *et al.*, 2005).

522

523 **ACKNOWLEDGEMENTS**

524 We acknowledge the work of countless collectors in the field and of the museum staff
525 responsible for the collections, our discussions with Scot Wing and Conrad Labandeira and
526 the technical support of Valerie Briand. AP profited from ATIP funding provided by the

527 CNRS. Comments by Michael Angilletta, Marl McPeek and two anonymous reviewers
528 substantially improved the manuscript.

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SUPPORTING INFORMATION

Appendix S1 Phylogenetic reconstruction

Appendix S2 Literature research: definitions, references, exploration of biases

Appendix S3 Robustness of the analysis to variation in underlying phylogenetic trees

BIOSKETCH

Andreas Prinzing studies the interface of habitat environments, past evolutionary diversification of species pools, and how this diversification controls, and is maintained by, present ecological interactions.

Author contributions: JFP and AP conceived the ideas with the collaboration of all other authors, JFP collected the data, CDH constructed the phylogeny, SP analysed the data, and JFP and AP took the lead role in the writing.

Editor: Melodie McGeoch

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Table 1. Use of harsh environments by *Willemia* species according to literature (references listed in Electronic Appendix S2). See text for more details on stress factors.

	Xeric	Hydric	Arctic	Alpine	Acid	Metallic	Saline	Tolerance breadth (salinity included)	Tolerance breadth (salinity excluded)
W. multilobata	√		√	√	√		√	5	4
W. bellingeri							√	1	0
W. trilobata	√							1	1
W. namibiae	√							1	1
W. similis	√		√	√	√			4	4
W. christianseni				√	√			2	2
W. anophthalma	√	√	√	√	√	√		6	6
W. dubia	√			√	√			3	3
W. scandinavica	√		√	√	√		√	5	4
W. koreana	√							1	1
W. iztaccihuatlensis				√	√			2	2
W. bedosae	√							1	1
W. unispina								0	0
W. psammophila							√	1	0
W. virae	√							1	1
W. tali	√							1	1
W. intermedia	√		√	√	√	√		5	5
W. shanghaiensis					√			1	1
W. granulata	√		√	√	√			4	4
W. fjellbergi			√					1	1
W. arida	√		√	√	√			4	4
W. trisphaerae			√	√	√			3	3
W. elisabethum					√			1	1
W. denisi	√	√	√	√	√			5	5
W. japonica								0	0
W. subbulbosa							√	1	0
W. persimilis								0	0
W. acantha								0	0
W. bulbosa								0	0
W. meybholae							√	1	0
W. arenicola							√	1	0
W. nepalensis					√			1	1
W. neocaledonica							√	1	0
W. nadchatrami								0	0
W. brevispina							√	1	0
W. annapurna								0	0
W. buddenbrocki								0	0
W. wandae								0	0
W. nosyboraha							√	1	0
W. delamarei								0	0
W. setonychia								0	0
W. deharvengi							√	1	0

780

FIGURE CAPTIONS

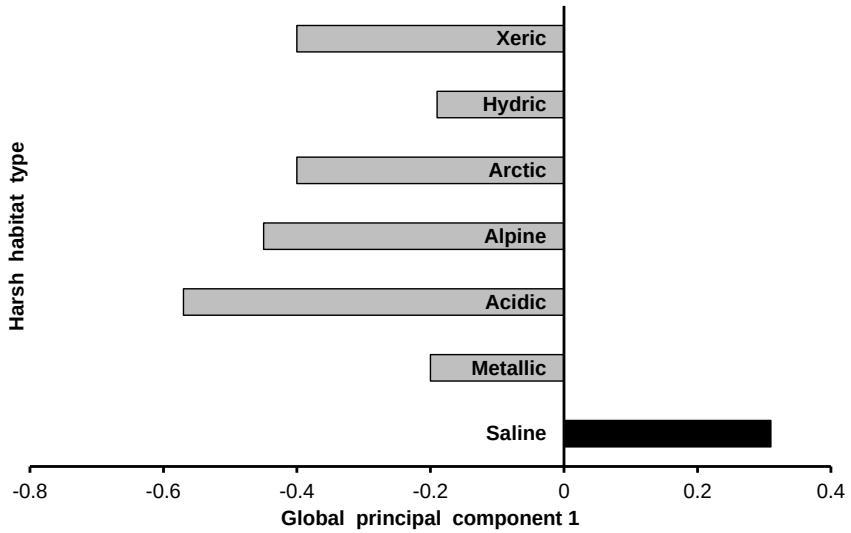
Figure 1. Ordination of correlations between uses of different types of harsh habitats, analysed by pPCA (a multivariate analysis based on phylogenetic distances). The coordinates of harsh habitat types are given along the first principal component. Note that except for salinity, the uses of habitats of all types of harshness are positively correlated.

Figure 2. Parsimony reconstruction of the use of harsh habitats, i.e., any type of harsh habitat used except for salinity (A), tropical distribution (B), and distribution on former Gondwana continents (C). The corresponding character states are shown in black. The tree shapes are not exactly identical because biogeographic distributions could not be assigned to either of the categories for a few species.

Figure 3. Clade ranks of species, i.e., nodal distances to the root, using different numbers of harsh habitat types. Error bar=S.E. Note that species that do not use any harsh habitats are at a greater distance from the root (see text for analyses).

Figure 4. Harshness breadth of species from tropical vs. non-tropical regions (a) and of species of Gondwanan vs. Laurasian origin (b). The few species of intermediate localisation were not included. Error bar=S.E.

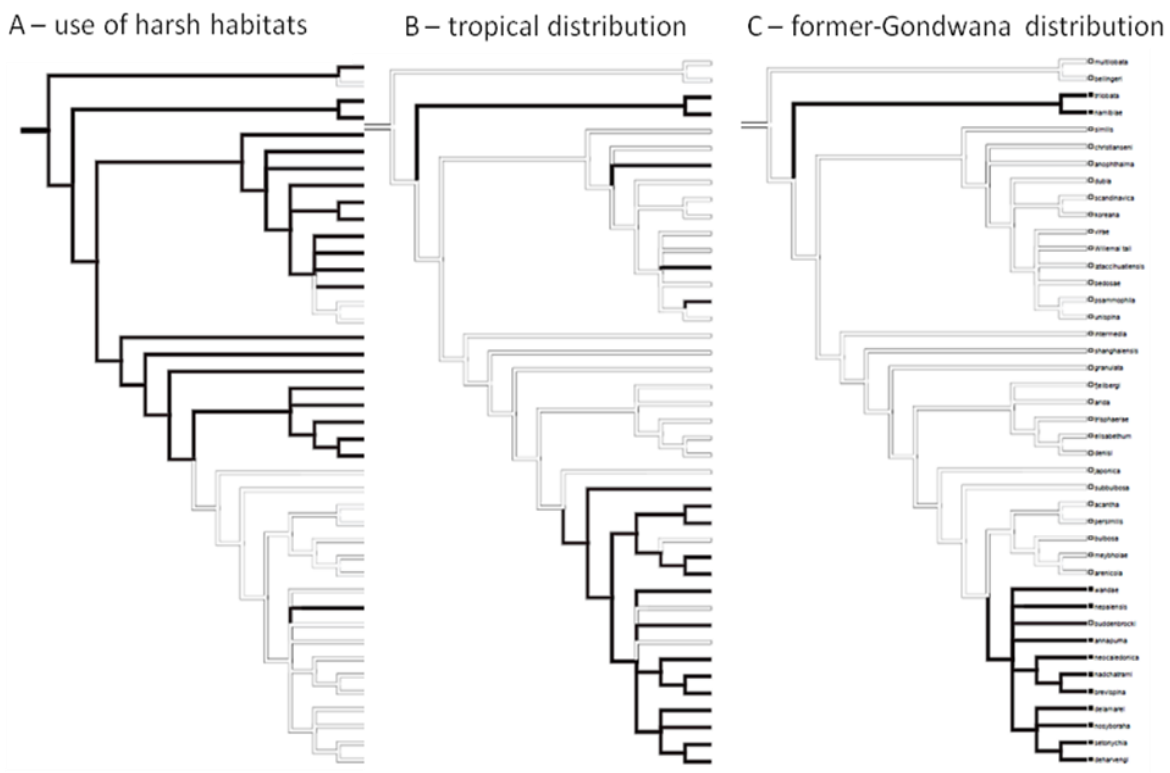
Figure 5. Clade ranks, i.e., distances to the root of the phylogenetic tree, in species from tropical vs. non-tropical regions (a) and from areas of Gondwanan vs. Laurasian origin (b). The few species with intermediate localisation were not included. Error bar=S.E. Note that the difference between Gondwanan vs. Laurasian origin disappears after including harshness breadth as a covariable (whereas harshness breadth is significant at p=0.011, *see text).*



805

806 Fig. 1

807



808

809 Fig. 2

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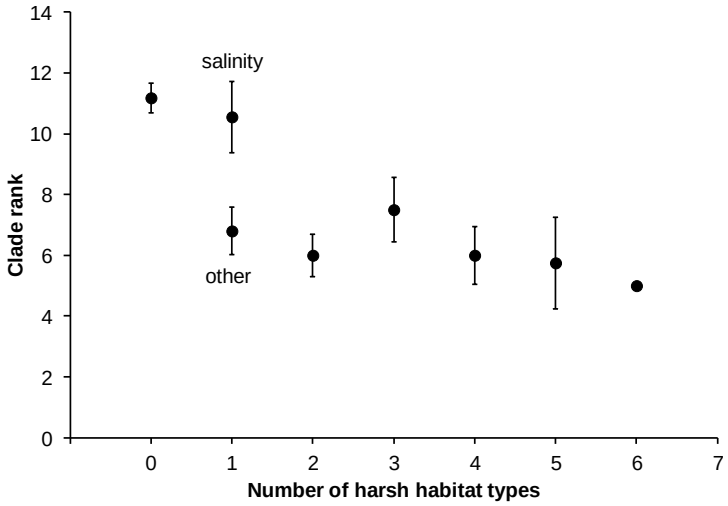

812

813 Fig. 3

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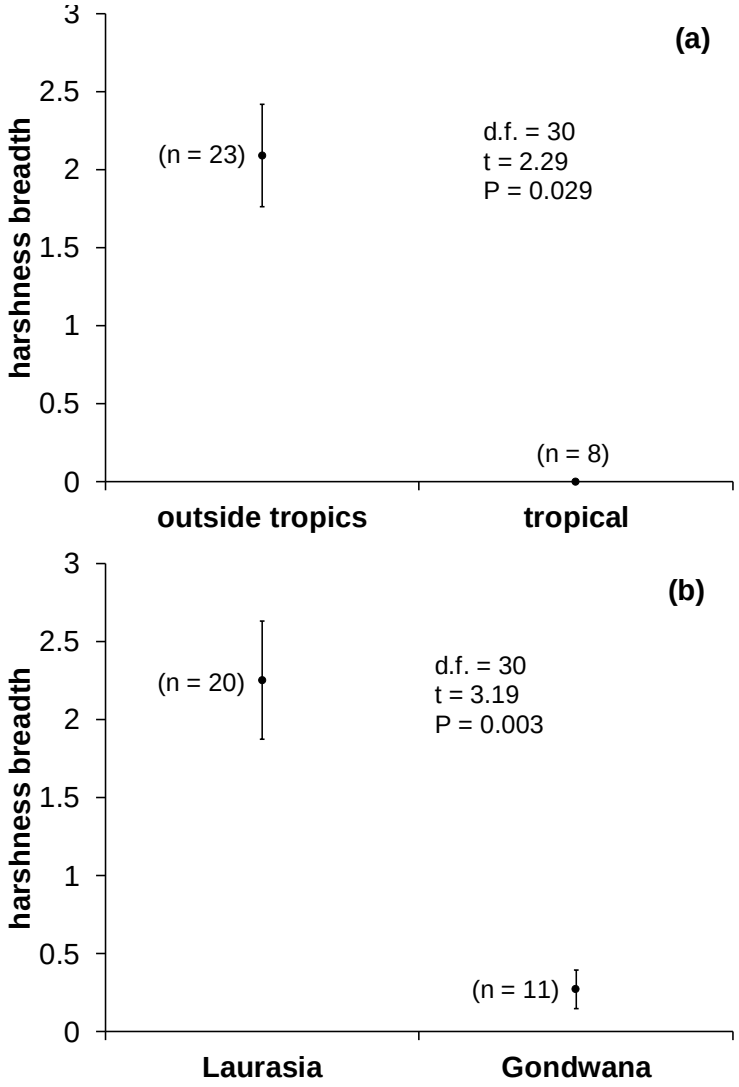
815



816

817 Fig. 4

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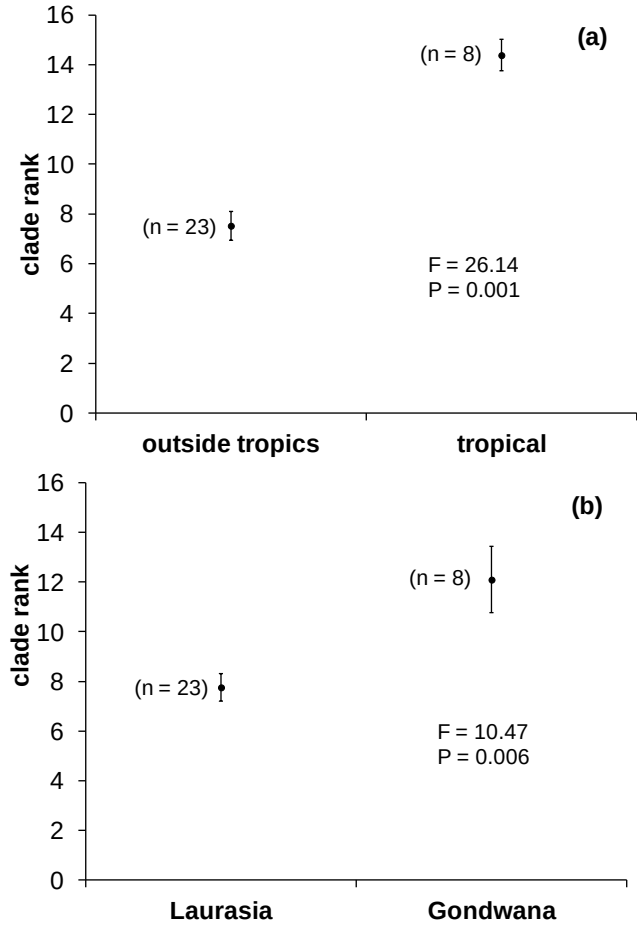

819

820 Fig. 5

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Appendix S1: Phylogenetic reconstruction

Appendix S1a: General approach

Within the Class Collembola the genus *Willemia* belongs to the Hypogastruridae family. It differs from other hypogastrurid genera by the total lack of pigment and furcula and the small size of the slender body, which never exceeds 1 mm in length (Thibaud, 2004). According to their life form all *Willemia* species belong to the euedaphobiont sub-category Bc3b (small size, slender body, no furcula) of Rusek (2007). The study deals with 42 of the 43 species worldwide known today in this genus (list below in Appendix S1b). The remaining species *W. biseta* Christiansen & Bellinger 1980 was excluded because it could not be studied in detail (see D'Haese 2000). Eight species have been added to the phylogenetic tree published by D'Haese (2000): *W. bulbosa* Bonet 1945, *W. acantha* Bonet 1945, *W. unispina* Fjellberg 2007, *W. iztaccihuatlensis* García Gómez & Cutz Pool 2008, *W. tali* Kaprus' & Nevo 2003, *W. psammophila* Palacios-Vargas & Thibaud 2001, *W. shanghaiensis* Yue 1999, and *W. nosybohara* Thibaud 2008.

Fifty-two morphological characters, which have been detailed in D'Haese (2000), were used for the phylogenetic analysis. Question marks (Appendix S1 b) represent either inapplicable or unknown characters. Autapomorphies, i.e. derived traits that are unique to a given terminal group, were excluded, so that only potentially informative characters were kept. All character states were polarized through comparison with three species belonging to the Hypogastruridae as outgroup: *Hypogastrura vernalis* Carl 1901, *Orogastrura dilatata* Cassagnau 1954, and *Xenyllogastrura octoculata* Steiner 1955.

We used morphological characters for reconstructing the phylogeny of the genus *Willemia*, because most species are rare and known only as collection specimens kept in conditions improper for molecular studies, a situation that often impedes worldwide

846 invertebrate molecular phylogenies if we limit ourselves to molecular characters (Turner et al.
847 2010). Moreover, it has been shown that phylogenies based on molecular and morphological
848 characters of extant species are in general largely congruent (Jablonski & Finarelli, 2009)
849 despite obvious discrepancies in particular cases. Finally, none of the 52 characters which
850 were used for the phylogeny of the genus *Willemia* (D'Haese, 2000) is related to use of harsh
851 environments. These characters concern chaetotactic setup of body and legs, which is of high
852 taxonomic value in most springtail families (including Hypogastruridae) but has little to do
853 with ecological adaptation (Gisin, 1967; Nayrolles, 1998; Rusek, 2002). The only exception is
854 pigmentation, absent from all *Willemia* species but present in the three outgroup species used
855 (*H. vernalis, O. dilatata, X. octoculata*). Thus there is no reason to believe that the use of
856 harsh environments, or a set characters correlated with it, was included in the reconstruction
857 of the phylogeny.

858 The data matrix (Appendix S1b) was analysed with POY version 4.1.2 (Varón *et al.*,
859 2010) through standard parsimony (static homology) with non-additive character coding
860 (unordered characters). The data matrix was submitted to a thousand replicates, ratchet
861 perturbation i.e. selection of 15% of characters upweighted by a factor of 3 at each iteration
862 (Nixon, 1999), tree fusing (Goloboff, 1999) and to a final branch swapping refinement
863 keeping up to 20% longer trees. Consistency (Kluge & Farris, 1969) and Retention Indices
864 (Farris, 1989) were calculated. Bremer (Bremer, 1988) and jackknife (Farris *et al.*, 1996)
865 branch support indices were computed.

866 For further calculations on phylogenetic relationships among *Willemia* species we
867 used a strict majority consensus tree based on six fully-resolved trees. The distance of each
868 species to the root was calculated by the number of nodes directly descending from the root to
869 it.

All data matrices, character list and analysis scripts can be found below in Appendix S1b and S1c.

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907

Appendix S1b: Data matrix of 52 characters in 3 outgroups and 42 species of the genus Willemia.

	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	Distance to the
H. vernalis	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	?	?	?	0	0	0	0	0	0	0	
O. dilatata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	1	0	0	0	?	?	0	0	0	
X. octoculata	0	0	0	0	0	0	0	1	0	0	0	?	0	1	0	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	?	1	0	0	0	?	0	0	0	0	
acantha	0	3	0	0	2	2	0	1	1	1	?	1	2	0	1	1	0	1	2	1	0	1	0	?	?	1	0	1	0	0	1	1	1	0	1	1	1	1	1	0	1	1	0	1	0	0	1	1	1	0	1	1	12
annapurna	1	0	0	3	0	0	3	1	1	1	1	1	3	1	1	1	0	1	3	1	0	0	1	3	3	1	0	1	0	0	0	1	1	0	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	0	1	1	12
anophthalma	1	0	0	0	0	0	0	1	1	0	0	0	1	0	1	1	0	1	0	1	0	0	0	1	1	1	0	1	0	0	0	1	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	6
arenicola	0	2	2	2	2	2	2	1	1	1	1	0	2	1	1	1	0	1	2	1	0	1	0	2	3	1	0	0	0	0	1	1	1	1	1	1	1	1	1	0	1	1	0	1	0	0	1	1	1	0	0	1	13
arida	1	3	3	2	2	2	2	1	1	0	?	1	0	0	1	1	0	1	0	1	0	0	0	?	?	1	0	1	0	0	0	1	1	0	0	0	0	1	1	0	1	1	0	1	0	1	1	0	0	0	0	1	1	9
bedosae	1	0	0	0	0	0	0	0	1	1	0	0	0	1	0	0	1	1	0	1	0	1	0	0	0	1	1	1	0	1	0	0	0	1	1	0	1	1	0	1	0	0	1	1	0	0	0	0	0	1	0	0	8
bellingeri	0	0	0	0	0	2	0	1	1	0	0	1	0	0	1	1	0	1	0	1	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	1	2
brevispina	1	3	0	3	2	0	3	1	1	1	1	1	3	1	1	1	1	1	0	1	0	0	1	2	2	1	0	1	0	0	0	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	14
buddenbrocki	1	0	0	3	0	0	3	1	1	1	1	1	3	1	1	1	1	1	2	1	0	0	1	3	3	1	0	1	0	0	0	1	1	0	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	0	1	1	13
bulbosa	0	3	2	2	2	2	2	1	1	1	?	1	2	0	1	1	0	1	0	1	0	1	0	?	?	1	0	1	0	0	0	1	1	1	0	1	1	1	1	1	0	1	1	0	1	0	0	1	1	1	0	0	1	12
christianseni	1	3	0	0	0	0	0	1	1	0	0	0	1	0	1	1	0	1	0	1	0	1	0	0	0	1	1	1	0	1	0	0	0	1	1	0	0	1	0	1	0	0	0	1	0	0	0	0	1	0	0	0	6
deharvengi	2	0	0	3	0	0	3	1	1	1	1	1	3	1	1	1	0	1	3	1	0	0	1	2	3	1	1	1	1	1	0	1	1	0	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	17
delamarei	1	0	0	3	0	0	3	1	1	?	?	?	?	1	1	1	0	1	2	1	0	0	1	?	?	1	1	1	1	1	0	1	1	0	1	1	1	1	1	1	1	1	1	?	?	?	?	?	1	?	?	?	0	1	16
denisi	1	1	1	1	1	1	1	1	1	0	0	1	0	0	1	1	1	1	0	1	0	1	0	1	1	1	0	1	0	0	1	1	1	0	1	1	1	1	1	0	1	1	0	1	0	1	1	0	0	0	1	1	10
dubia	1	0	0	0	0	0	0	0	1	1	0	0	0	1	0	1	1	0	1	0	1	0	0	0	1	1	1	0	1	0	0	0	1	1	0	1	1	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0	7
elisabethum	1	1	1	1	2	1	1	1	1	0	0	1	0	0	1	1	1	1	0	1	0	1	0	1	1	1	1	0	1	0	0	1	1	1	1	1	1	1	0	1	1	0	1	0	1	1	0	0	0	0	1	1	10
fjellbergi	1	3	3	2	2	2	2	1	1	0	0	1	0	0	1	1	0	1	0	1	0	0	0	1	1	1	0	1	0	0	0	1	1	0	0	0	0	1	1	0	1	1	?	1	?	1	1	0	0	0	1	1	9
granulata	1	0	0	0	2	2	0	1	1	0	0	1	0	0	1	1	0	1	0	1	0	1	0	0	0	1	1	1	0	1	0	0	0	1	1	0	0	0	0	1	1	0	1	0	0	1	0	0	0	1	1	6
intermedia	1	3	0	0	0	0	0	1	1	0	0	1	0	0	1	1	0	1	0	1	0	1	0	0	0	1	1	1	0	1	0	0	0	1	1	0	0	0	0	1	1	0	1	0	1	0	0	1	0	0	0	0	4
iztaccihuatlensis	1	1	0	0	0	0	0	1	1	0	0	0	1	0	1	1	0	1	0	1	0	1	0	0	0	?	?	1	0	1	0	0	1	1	1	0	1	1	0	1	?	0	1	1	0	0	?	0	1	0	0	0	0	7
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meybholae	0	2	2	2	2	2	2	1	1	1	1	1	2	1	1	1	0	1	3	1	0	1	0	2	3	1	0	0	0	0	1	1	1	1	1	1	1	1	0	1	1	0	1	0	0	1	1	1	0	1	1	1	13
multilobata	0	0	0	0	0	2	0	1	1	0	0	1	0	0	?	?	0	1	0	1	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	1	0	0	0	2
nadchatrami	1	0	0	3	0	0	3	1	1	1	1	1	3	1	1	1	1	1	0	1	0	0	1	2	2	1	0	0	0	0	0	1	1	0	1	1	1	1	1	?	0	1	1	1	1	1	1	?	?	1	0	1	14
namibiae	0	0	0	0	0	0	0	1	1	0	0	1	1	0	1	1	0	1	0	?	1	?	0	2	3	1	0	0	0	0	0	1	0	0	1	1	0	1	0	0	0	0	?	1	0	0	1	0	0	?	0	1	3
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nepalensis	1	0	0	3	0	0	3	1	1	1	1	1	3	1	1	1	0	1	2	1	0	0	1	2	2	1	1	1	0	0	0	1	1	0	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	0	1	1	12
nosyboraha	1	0	0	3	0	0	3	1	1	1	1	?	?	1	1	1	1	1	1	1	0	0	1	3	3	1	1	1	1	1	0	1	1	0	1	1	1	1	1	1	1	1	0	0	1	0	?	?	?	?	0	1	15
persimilis	0	3	0	0	2	2	0	1	1	1	?	1	2	0	1	1	0	1	2	1	0	1	0	?	?	1	0	1	0	0	0	1	1	1	0	1	1	1	1	1	0	1	1	0	1	0	0	0	1	1	1	0	0	1	12
psammophila	0	0	0	0	0	0	0	1	1	1	0	0	1	0	1	1	0	1	1	1	0	0	0	3	3	1	1	1	1	1	0	1	0	0	0	1	0	1	?	0	1	1	0	0	0	0	0	1	?	0	0	0	10
scandinavica	1	0	0	0	2	2	0	1	1	0	0	0	1	0	1	1	0	1	0	1	0	0	0	1	1	1	0	?	0	0	0	1	1	0	1	1	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	8
setonychia	2	0	0	3	0	0	3	1	1	?	?	?	?	1	1	1	0	1	3	1	0	?	?	?	?	1	1	1	1	1	0	1	1	0	1	1	1	1	1	1	1	1	?	?	?	?	1	?	?	?	1	1	17
shanghaiensis	1	0	0	0	2	2	0	1	1	?	?	?	?	?	?	?	?	1	0	1	0	0	0	0	?	?	1	0	0	0	0	0	1	1	0	0	0	0	?	?	0	1	1	?	?	?	?	1	?	?	0	0	1	5
similis	1	0	0	0	0	0	0	0	1	1	0	0	1	1	0	1	1	0	1	0	1	0	0	0	1	1	1	0	1	0	0	0	0	1	0	0	1	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0	4
subbulbosa	1	2	2	2	2	2	2	1	1	1	1	1	2	0	1	1	0	1	0	1	0	0	0	2	3	1	0	1	0	0	0	1	1	0	0	1	0	1	1	0	1	1	0	1	0	0	1	1	1	0	0	1	9
tali	1	1	1	1	?	0	1	1	1	0	0	0	1	0	1	1	0	1	0	1	0	0	0	1	1	1	1	1	0	0	0	1	1	0	1	1	1	1	1	1	1	1	0	0	0	0	0	1	1	0	0	0	10
trilobata	0	0	0	0	0	0	0	1	1	0	0	0	1	1	0	1	1	0	1	0	?	1	0	0	2	3	1	0	0	0	0	0	1	0	0	1	1	0	1	0	0	0	0	0	?	1	0	0	1	?	?	?	3
trisphaerae	1	3	1	1	2	2	1	1	1	0	0	1	0	0	1	1	?	1	0	1	0	0	0	1	1	1	0	1	0	0	0	1	1	0	0	0	0	1	1	0	1	1	0	1	0	1	1	0	0	0	1	1	9
unispina	1	0	0	0	0	0	0	0	1	?	?	1	0	0	1	1	?	1	0	1	0	1	0	0	0	1	1	1	1	1	1	1	0	1	1	1	0	1	1	0	1	0	0	1	1	0	0	0	0	1	?	?	0	1	1	10
virae	1	0	0	0	0	0	0	0	1	1	0	0	0	1	0	1	1	0	1	0	1	0	0	0	1	1	1	0	1	0	0	0	1	1	0	1	1	1	1	0	0	0	1	1	?	0	0	0	1	0	0	0	0	1	10
wandae	1	0	0	3	0	0	3	1	1	1	1	1	3	1	1	1	1	1	2	1	0	0	1	3	3	1	1	1	0	0	0	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	14

Appendix S1c: Files used for the construction of the strict consensus phylogenetic tree.

Printout of files used by Cyrille d'Haese for the construction of the strict consensus phylogenetic tree (Fig. 1). The file will-bre1.trees needed to calculate bremer support is not provided because of its size (~58Mo). All these files are available upon request at dhaese@mnhn.fr

The following file willemia2000.ss is the original data matrix from D'Haese (2000) in Hennig86 format:

```
xread
'Matrix of DHaese, C. Is psammophily an evolutionary dead end? a
phylogenetic test in the genus Willemia (Collembola: Hypogastruridae)
Cladistics, 2000, 16, 255-273'
52 37
Hypogastrura_vernalis
      000000000?00000000000000000000000000000010???000000
Orogastrura_dilatata
      00000000000000000000000000000000000010100010100??000
Xenyllogastrura_octoculata
      00000001000?01000000010110000000000000010010?1000?0000
Willemia_annapurna
      10030031111131110131001331010001101111111101111111101
Willemia_anophthalma
      10000001100010110101000111010001000101000100001000001
Willemia_arenicola
      02222221111021110121010231000011111111101101001110001
Willemia_arida
      1332222110?100110101000??10100011000011011010110001 1
Willemia_bedosae
      10000001100010110101000111010001101101001100001000001
Willemia_bellingeri
      00000201100100110101000111000000000000000010100100001
Willemia_brevispina
      13032031111131111101001221010001101111111111111111101
Willemia_buddenbrocki
      10030031111131111121001331010001101111111101111111101
Willemia_christianseni
      13000001100010110101000111010001100101000100001000001
Willemia_deharvengi
      20030031111131110131001231111101101111111101111111111
Willemia_delamarei
      100300311????1110121001??111110110111111111????1???01
Willemia_denisi
      11111111100100111101010111010011101111101101011000 11
Willemia_dubia
      10000001100010110101000111010001101101000100001000001
Willemia_elisabethum
      11112111100100111101010111010011101111101101011000 11
Willemia_fjellbergi
      13322221100100110101000111010001100001101 1?1100011
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Willemia_granulata
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Willemia_intermedia
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Willemia_japonica
      10022221100100110101000111010001100101101101001000011
Willemia_koreana
      10002201100010110101000111010001101101000100001000011
Willemia_meybholae
      02222221111121110131010231000011111111101101001110111
Willemia_multilobata
      00000201100100??0101000111000000000000000010100100001
Willemia_nadchatrami
      10030031111131111101001221000001101111?0111111??101
Willemia_namibiae
      00000001100110110101?1?02310000010011010000?100100?01
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Willemia_nepalensis
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Willemia_persimilis
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Willemia_scandinavica
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Willemia_setonychia
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Willemia_similis
      10000001100110110101000111010000100101000100001000011
Willemia_subbulbosa
      12222221111120110101000231010001100101101101001110011
Willemia_trilobata
      00000001100110110101?10023100000100110100000?1001???01
Willemia_trisphaerae
      13112211100100111?10100011101000110000110110101100011
Willemia_virae
      10000001100010110101000111010001101111001100010000011
Willemia_wandae
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ccode - 0.51;
proc /;
;
cn
{0 On_antennal_segment_IV,_apical_vesicle large small absent;
{1 Sensilla_e1_on_antennal_segment_IV subcylindrical_(Figs._2A_and_2D)
candle_flame-shaped_(Fig._2B) globular_(Fig._2C)
not_differentiated_from_ordinary_setae;
{2 Sensilla_e2_on_antennal_segment_IV subcylindrical_(Figs._2A_and_2D)
candle_flame-shaped_(Fig._2B) globular_(Fig._2C)
not_differentiated_from_ordinary_setae;
{3 Sensilla_e3_on_antennal_segment_IV subcylindrical_(Fig._2A)
candle_flame-shaped_(Fig._2B) globular_(Fig._2C)
globular_in_cavity_(Fig._2D);
{4 Sensilla_d_on_antennal_segment_IV subcylindrical_(Figs._2A_and_2D)
candle_flame-shaped not_differentiated_from_ordinary_setae_(Fig._2C);
{5 Sensilla_i1_on_antennal_segment_IV subcylindrical_(Figs._2A_and_2D)
candle_flame-shaped_(Fig._2B)
not_differentiated_from_ordinary_setae_(Fig._2C);
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{6 Sensilla_i2_on_antennal_segment_IV subcylindrical_(Fig._2A)
candle_flame-shaped_(Fig._2B) globular_(Fig._2C)
globular_in_cavity_(Fig._2D);
{7
Small_internal_sensilla_of_sensory_organ_of_antennal_segment_III_(Figs.
_2A_to_2D) free covered_in_part_by_a_tegumental_fold;
{8 Third_and_fourth_antennal_segments clearly_separated
ventrally_slightly_fused;
{9 Antennal_segment_II_with 12_setae 11_setae;
{10 Antennal_segment_I_with 7_setae 6_setae;
{11 Prelabral_chaetotaxy_with 4_setae 2_setae;
{12 Labral_chaetotaxy_with 5.5.4_setae 4.5.4_setae 2.5.4_setae
5.3.4_setae;
{13 Seta_a0_on_the_head present_(Fig._1A) absent_(Fig._1B);
{14 Number_of_setae_d_on_the_head: 5_+_5 4_+_4_(Figs._1A_and_1B);
{15 Number_of_setae_v_on_the_head: 2_+_2 1_+_1_(Figs._1A_and_1B);
{16 Setae_c1_on_the_head present absent;
{17 Corneules present absent;
{18 Postantennal_organ_with 4_to_9_vesicles_(Fig._1A) 10_to_15_vesicles
more_than_15_vesicles_(Fig._1B);
{19 Setae_a1_of_thoracic_tergum_III_positioned on_thoracic_tergum_III
between_thoracic_terga_II_and_III_(Figs._1A_and_1B);
{20 On_second_and_third_thoracic_terga,_setae_a1 present absent;
{21 On_thoracic_terga_II_and_III,_setae_a2 present absent;
{22 On_thoracic_terga_II_and_III,_setae_m3 present_(Fig._1A)
absent_(Fig._1B);
{23 Tibiotarsi_I_and_II_with 19_setae 17_setae 12_setae 11_setae;
{24 Tibiotarsus_III_with 18_setae 16_setae 12_setae 11_or_10_setae;
{25 Tibiotarsi with_tenent_hair without_tenent_hair;
{26 On_thoracic_tergum_III,_setae_s_(=m7) subcylindrical_and_acuminate
lanceolate;
{27 On_abdominal_terga_II_and_III,_setae_s
subcylindrical_and_acuminate_(Fig._1A) lanceolate_(Fig._1B);
{28 On_abdominal_tergum_IV,_setae_s subcylindrical_and_acuminate
lanceolate;
{29 On_abdominal_tergum_V,_setae_s subcylindrical_and_acuminate
lanceolate;
{30 On_abdominal_terga_II_and_III,_setae_a2 present absent;
{31 On_abdominal_terga_II_and_III,_setae_m2 present_(Fig._1A)
absent_(Fig._1B);
{32 On_abdominal_terga_II_and_III,_setae_m3 present absent;
{33 On_abdominal_terga_I_II_and_III,_tegumentary_granulation normal
coarse_secondary_granulation_near_setae_s;
{34 On_abdominal_tergum_IV,_setae_m1 present_(Fig._1A)
absent_(Fig._1B);
{35 On_abdominal_tergum_IV,_setae_m2 present absent;
{36 On_abdominal_tergum_IV,_setae_m3 present_(Fig._1A)
absent_(Fig._1B);
{37 On_abdominal_tergum_IV,_setae_m3' present absent;
{38 On_abdominal_tergum_IV,_setae_p5 present_(Fig._1A)
absent_(Fig._1B);
{39 On_abdominal_tergum_V,_setae_a3 present_(Fig._1A) absent_(Fig._1B);
{40 On_abdominal_tergum_V,_setae_s
in_p3_position_i.e._p2_present_(Fig._1A)
in_p2_position_i.e._p2_absent_(Fig._1B);
{41 Ventral_tube_with more_than_4_+_4_setae with_4_1_4_setae;
{42 On_abdominal_sternum_II,_setae_a3 present absent;

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{43 On_abdominal_sternum_IV,_setae_a1 present_(Fig._3A)
absent_(Fig._3B);
{44 On_abdominal_sternum_IV, 4_rows_of_setae_(Fig._3A)
3_rows_of_setae_(Fig._3B);
{45 On_abdominal_sternum_IV,_setae_m1 present absent;
{46 Furca present absent;
{47 On_anal_lobes,_setae_e present_(Fig._4A) absent_(Fig._4B);
{48 On_anal_lobes,_setae_z present_(Fig._4A) absent_(Fig._4B);
{49 On_anal_lobes,_distal_setae_of_hr_group present_(Fig._4A)
absent_(Fig._4B);
{50 Anal_spines present absent;
{51 Pigmentation present absent;
;
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The following file willemia2011_char.ss is the new matrix with 5 Willemia species added along with the character list:

```
xread
' Matrix of Ponge et al based on DHaese 2000 (Is psammophily an
evolutionary dead end? Cladistics) with new species added '
52 45
Hypogastrura_vernalis
      000000000?00000000000000000000000000000010???000000
Orogastrura_dilatata
      00000000000000000000000000000000000010100010100??000
Xenyllogastrura_octoculata
      000000010000?0100000001011000000000000010010?1000?0000
Willemia_annapurna
      10030031111131110131001331010001101111111101111111101
Willemia_anophthalma
      10000001100010110101000111010001000101000100001000001
Willemia_arenicola
      02222221111021110121010231000011111111101101001110001
Willemia_nosyboraha
      10030031111??11111110013311111011011111111100010???01
Willemia_arida   133222211O?100110101000??10100011000011011010110001l
Willemia_bedosae 10000001100010110101000111010001101101001100001000001
Willemia_bellingeri
      00000201100100110101000111000000000000000010100100001
Willemia_brevispina
      13032031111131111101001221010001101111111111111111101
Willemia_buddenbrocki
      10030031111131111121001331010001101111111101111111101
Willemia_christianseni
      13000001100010110101000111010001100101000100001000001
Willemia_deharvengi
      20030031111131110131001231111101101111111101111111111
Willemia_delamarei
      1003003111???111012100l??11111011011111111????1???01
Willemia_denisi  11111111100100111101010111010011101111101101011000ll
Willemia_dubia   10000001100010110101000111010001101101000100001000001
Willemia_elisabethum
      11112111100100111101010111010011101111101101011000ll
Willemia_fjellbergi
      13322221100100110101000111010001100001101l?1?1100011
Willemia_unispina100000001??10011?10100011111110110110100110000l??011
Willemia_granulata
      10002201100100110101000111010001100001101101001000ll
Willemia_intermedia
      13000001100100110101000111010001100001101101001000001
Willemia_iztaccihuatlensis  11000001100010110101000[1-2][1-
2]10100111011O1?01100?0100001
Willemia_japonica10022221100100110101000111010001100101101101001000ll
Willemia_koreana 10002201100010110101000111010001101101000100001000001
Willemia_meybholae
      02222221111121110131010231000011111111101101001110ll
Willemia_multilobata
      000002011001O0??01010001110000000000000000101001000001
Willemia_nadchatrami
      10030031111131111101001221000001101111l?0111111??101
Willemia_namibiae0000000110011011010?1?023100000100110100O0?100100?01
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Willemia_nepalensis
      10030031111131110121001221110001101111111101111111101
Willemia_persimilis
      0300220111?120110121010??10100111011111101101001110 01
Willemia_psammophila
      00000001110010110111000331111101000101?01100001?0001
Willemia_bulbosa 0322222111?1201101[0-
1]1010??10100111011111101101001110 01
Willemia_acantha 0300220111?120110121010??10100111011111101101001110 11
Willemia_scandinavica
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Willemia_setonychia
      200300311????1110131 0????1111101101111111????1???11
Willemia_shanghaiensis
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Willemia_similis 10000001100110110101000111010000100101000100001000 01
Willemia_subbulbosa
      12222221111120110101000231010001100101101101001110 01
Willemai_tali    1111?01110001011010100011111000110111100110000110001
Willemia_trilobata
      00000001100110110 10?10023100000100110100 00?1001???01
Willemia_trisphaerae
      13112211100100 11?10100011101000110000110110101100011
Willemia_virae   10000001100010110101000111010001101111001 1?000100001
Willemia_wandae  10030031111131111121001331110001101111111111111111101
;

ccode - 0.51;
proc/;

;
cn
{0 On_antennal_segment_IV,_apical_vesicle large small absent;
{1 Sensilla_e1_on_antennal_segment_IV subcylindrical_(Figs._2A_and_2D)
candle_flame-shaped_(Fig._2B) globular_(Fig._2C)
not_differentiated_from_ordinary_setae;
{2 Sensilla_e2_on_antennal_segment_IV subcylindrical_(Figs._2A_and_2D)
candle_flame-shaped_(Fig._2B) globular_(Fig._2C)
not_differentiated_from_ordinary_setae;
{3 Sensilla_e3_on_antennal_segment_IV subcylindrical_(Fig._2A)
candle_flame-shaped_(Fig._2B) globular_(Fig._2C)
globular_in_cavity_(Fig._2D);
{4 Sensilla_d_on_antennal_segment_IV subcylindrical_(Figs._2A_and_2D)
candle_flame-shaped not_differentiated_from_ordinary_setae_(Fig._2C);
{5 Sensilla_i1_on_antennal_segment_IV subcylindrical_(Figs._2A_and_2D)
candle_flame-shaped_(Fig._2B)
not_differentiated_from_ordinary_setae_(Fig._2C);
{6 Sensilla_i2_on_antennal_segment_IV subcylindrical_(Fig._2A)
candle_flame-shaped_(Fig._2B) globular_(Fig._2C)
globular_in_cavity_(Fig._2D);
{7
Small_internal_sensilla_of_sensory_organ_of_antennal_segment_III_(Figs.
_2A_to_2D) free covered_in_part_by_a_tegumental_fold;
{8 Third_and_fourth_antennal_segments clearly_separated
ventrally_slightly_fused;
{9 Antennal_segment_II_with 12_setae 11_setae;
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{10 Antennal_segment_I_with 7_setae 6_setae;
{11 Prelabral_chaetotaxy_with 4_setae 2_setae;
{12 Labral_chaetotaxy_with 5.5.4_setae 4.5.4_setae 2.5.4_setae
5.3.4_setae;
{13 Seta_a0_on_the_head present_(Fig._1A) absent_(Fig._1B);
{14 Number_of_setae_d_on_the_head: 5_+_5 4_+_4_(Figs._1A_and_1B);
{15 Number_of_setae_v_on_the_head: 2_+_2 1_+_1_(Figs._1A_and_1B);
{16 Setae_c1_on_the_head present absent;
{17 Corneules present absent;
{18 Postantennal_organ_with 4_to_9_vesicles_(Fig._1A) 10_to_15_vesicles
more_than_15_vesicles_(Fig._1B);
{19 Setae_a1_of_thoracic_tergum_III_positioned on_thoracic_tergum_III
between_thoracic_terga_II_and_III_(Figs._1A_and_1B);
{20 On_second_and_third_thoracic_terga,_setae_a1 present absent;
{21 On_thoracic_terga_II_and_III,_setae_a2 present absent;
{22 On_thoracic_terga_II_and_III,_setae_m3 present_(Fig._1A)
absent_(Fig._1B);
{23 Tibiotarsi_I_and_II_with 19_setae 17_setae 12_setae 11_setae;
{24 Tibiotarsus_III_with 18_setae 16_setae 12_setae 11_or_10_setae;
{25 Tibiotarsi with_tenent_hair without_tenent_hair;
{26 On_thoracic_tergum_III,_setae_s_(=m7) subcylindrical_and_acuminate
lanceolate;
{27 On_abdominal_terga_II_and_III,_setae_s
subcylindrical_and_acuminate_(Fig._1A) lanceolate_(Fig._1B);
{28 On_abdominal_tergum_IV,_setae_s subcylindrical_and_acuminate
lanceolate;
{29 On_abdominal_tergum_V,_setae_s subcylindrical_and_acuminate
lanceolate;
{30 On_abdominal_terga_II_and_III,_setae_a2 present absent;
{31 On_abdominal_terga_II_and_III,_setae_m2 present_(Fig._1A)
absent_(Fig._1B);
{32 On_abdominal_terga_II_and_III,_setae_m3 present absent;
{33 On_abdominal_terga_I_II_and_III,_tegumentary_granulation normal
coarse_secondary_granulation_near_setae_s;
{34 On_abdominal_tergum_IV,_setae_m1 present_(Fig._1A)
absent_(Fig._1B);
{35 On_abdominal_tergum_IV,_setae_m2 present absent;
{36 On_abdominal_tergum_IV,_setae_m3 present_(Fig._1A)
absent_(Fig._1B);
{37 On_abdominal_tergum_IV,_setae_m3' present absent;
{38 On_abdominal_tergum_IV,_setae_p5 present_(Fig._1A)
absent_(Fig._1B);
{39 On_abdominal_tergum_V,_setae_a3 present_(Fig._1A) absent_(Fig._1B);
{40 On_abdominal_tergum_V,_setae_s
in_p3_position_i.e._p2_present_(Fig._1A)
in_p2_position_i.e._p2_absent_(Fig._1B);
{41 Ventral_tube_with more_than_4_+_4_setae with_4_1_4_setae;
{42 On_abdominal_sternum_II,_setae_a3 present absent;
{43 On_abdominal_sternum_IV,_setae_a1 present_(Fig._3A)
absent_(Fig._3B);
{44 On_abdominal_sternum_IV, 4_rows_of_setae_(Fig._3A)
3_rows_of_setae_(Fig._3B);
{45 On_abdominal_sternum_IV,_setae_m1 present absent;
{46 Furca present absent;
{47 On_anal_lobes,_setae_e present_(Fig._4A) absent_(Fig._4B);
{48 On_anal_lobes,_setae_z present_(Fig._4A) absent_(Fig._4B);
{49 On_anal_lobes,_distal_setae_of_hr_group present_(Fig._4A)
absent_(Fig._4B);
```

```
{50 Anal_spines present absent;
{51 Pigmentation present absent;
;
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The following file willemia2011.ss is the same data matrix but without the character list to be directly readable by POY:

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xread
' Matrix of Ponge et al based on DHaese 2000 (Is psammophily an
evolutionary dead end? Cladistics) with new species added '
52 45
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      000000000?0000000000000000000000000000010???000000
Orogastrura_dilatata
      00000000000000000000000000000000001010001010000??000
Xenyllogastrura_octoculata
      000000010000?0100000001011000000000000010010?1000?0000
Willemia_annapurna
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Willemia_anophthalma
      1000000110001011010100011101000100010100010000100001
Willemia_arenicola
      022222211110211101210102310000111111111010100111001
Willemia_nosyboraha
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Willemia_arida   133222211O?100110101000??10100011000011011010110001l
Willemia_bedosae 1000000110001011010100011101000110110100110000100001
Willemia_bellingeri
      000002011001001101010001110000000000000000010100100001
Willemia_brevispina
      130320311111311111010012210100011011111111111111101
Willemia_buddenbrocki
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Willemia_christianseni
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Willemia_dubia   1000000110001011010100011101000110110100010000100001
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Willemia_intermedia
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Willemia_iztaccihuatlensis  11000001100010110101000[1-2][1-
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Willemia_japonica100222211001001101010001110100011001011011010010001l
Willemia_koreana 1000220110001011010100011101000110110100010000100001
Willemia_meybholae
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Willemia_multilobata
      000002011001OO??0101000111000000000000000010100100001
Willemia_nadchatrami
      100300311111311111010012210000011011111?0111111??101
Willemia_namibiae0000000110011011010?1?023100000100110100O?100100?01
```

```
Willemia_neocaledonica
      1003003111113111112100122101000110111111111111111101
Willemia_nepalensis
      1003003111113111012100122111000110111111110111111101
Willemia_persimilis
      0300220111?120110121010??10100111011111010110011101
Willemia_psammophila
      0000000111001011011100033111110100010?01100001?0001
Willemia_bulbosa 0322222111?1201101[0-
1]1010??10100111011111010110011101
Willemia_acantha 0300220111?120110121010??101001110111110110100111011
Willemia_scandinavica
      1000220110001011010100011 10?000110110100010000100001
Willemia_setonychia
      200300311????1110131 0????111110110111111 1????1???11
Willemia_shanghaiensis
      100022011????????101000??100000110000??011????1??001
Willemia_similis 1000000110011011010100011101000010010100010000100001
Willemia_subbulbosa
      1222222111112011010100023101000110010110110100111001
Willemai_tali    1111?011100010110101000111110001101111001100001100 01
Willemia_trilobata
      000000011001101101 0?10023100000100110100 00?1001???01
Willemia_trisphaerae
      131122111001001 1?10100011101000110000110110101100011
Willemia_virae   1000000110001011010100011101000110111100 11?000100001
Willemia_wandae  1003003111113111112100133111000110111111111111111101
;

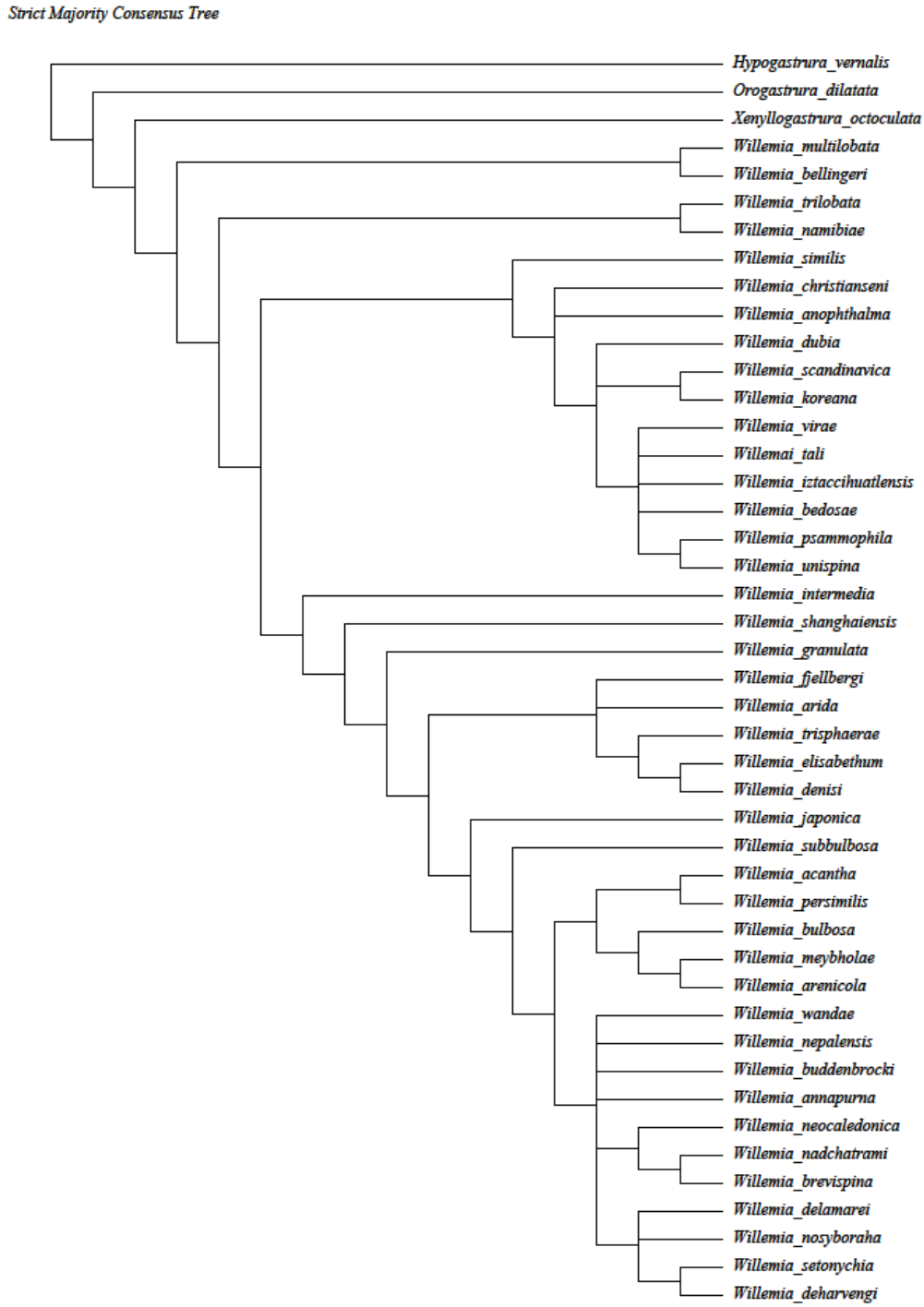
ccode - 0.51;
proc/;
```

The following file will.sh is the main analysis script for POY:

```
wipe ()
read ("willemia2011.ss")
set (root: "Hypogastrura_vernalis")
build (1000)
select (unique)
perturb (iterations:2, ratchet:(0.15,3), swap(tbr, trees:2))
select (unique)
fuse ()
select (unique)
swap (threshold:20)
swap (all, visited:"will-bre1.trees", timeout:3600)
select ()
report ("will.tre", trees:(total))
report ("will_results.ss", phastwinclad, trees:(hennig, total))
report ("will-cons.tre", consensus, "will-cons", graphconsensus)
report ("will-stats.txt", treestats, ci, ri)
report ("will-diag.txt", diagnosis)
exit ()
```

will-cons.pdf (consensus in pdf format), will-cons.tre (consensus in text format), will-stats (tree length ci and ri), and will.tre (the six equally parsimonious trees) are the results of the analysis.

will-cons.pdf:



will-cons.tre:

```
Strict Majority Consensus Tree
(Hypogastrura_vernalis,(Orogastrura_dilatata,(Xenyllogastrura_octoculat
a,((Willemia_multilobata,Willemia_bellingeri),((Willemia_trilobata,Will
emia_namibiae),((Willemia_similis,(Willemia_christianseni,Willemia_anop
hthalma,(Willemia_dubia,(Willemia_scandinavica,Willemia_koreana),(Wille
mia_virae,Willemai_tali,Willemia_iztaccihuatlensis,Willemia_bedosae,(Wi
llemia_psammophila,Willemia_unispina))))),(Willemia_intermedia,(Willemi
a_shanghaiensis,(Willemia_granulata,((Willemia_fjellbergi,Willemia_arid
a,(Willemia_trisphaerae,(Willemia_elisabethum,Willemia_denisi))),(Wille
mia_japonica,(Willemia_subbulbosa,(((Willemia_acantha,Willemia_persimil
is),(Willemia_bulbosa,(Willemia_meybholae,Willemia_arenicola))),(Willem
ia_wandae,Willemia_nepalensis,Willemia_buddenbrocki,Willemia_annapurna,
(Willemia_neocaledonica,(Willemia_nadchatrami,Willemia_brevispina)),(Wi
llemia_delamarei,Willemia_nosyboraha,(Willemia_setonychia,Willemia_deha
rvengi))))))))))))))))
```

will-stats:

```
Trees Found:

               Tree length    Number of hits
               154.           6
CI Statistics:

                 Tree Cost CI
                 154.      46.1038961039
                 154.      46.1038961039
                 154.      46.1038961039
                 154.      46.1038961039
                 154.      46.1038961039
                 154.      46.1038961039
RI Statistics:

                 Tree Cost RI
                 154.      82.3404255319
                 154.      82.3404255319
                 154.      82.3404255319
                 154.      82.3404255319
                 154.      82.3404255319
                 154.      82.3404255319
```

will.tre:

```
(Hypogastrura_vernalis,(Orogastrura_dilatata,(Xenyllogastrura_octoculat
a
,((Willemia_multilobata,Willemia_bellingeri),((Willemia_trilobata
,Willemia_namibiae),((Willemia_similis,((Willemia_christianseni
,Willemia_anophthalma),((Willemia_dubia,(Willemia_scandinavica
,Willemia_koreana)),(Willemia_iztaccihuatlensis,(Willemia_bedosae
,((Willemia_unispina,Willemia_psammophila),(Willemia_virae,Willemai_tal
i)))))
)),(Willemia_intermedia,(Willemia_shanghaiensis,(Willemia_granulata
,(((Willemia_fjellbergi,Willemia_arida),(Willemia_trisphaerae
,(Willemia_elisabethum,Willemia_denisi))),(Willemia_japonica
,(Willemia_subbulbosa,(((Willemia_persimilis,Willemia_acantha)
,(Willemia_bulbosa,(Willemia_meybholae,Willemia_arenicola)))
,((Willemia_nepalensis,(Willemia_neocaledonica,(Willemia_nadchatrami
,Willemia_brevispina))),(Willemia_annapurna,(Willemia_buddenbrocki
,(Willemia_wandae,(Willemia_nosyboraha,(Willemia_delamarei
,(Willemia_setonychia,Willemia_deharvengi))))))))))))))))[154.];
(Hypogastrura_vernalis,(Orogastrura_dilatata,(Xenyllogastrura_octoculat
a
,((Willemia_multilobata,Willemia_bellingeri),((Willemia_trilobata
,Willemia_namibiae),((Willemia_similis,((Willemia_christianseni
,Willemia_anophthalma),((Willemia_dubia,(Willemia_scandinavica
,Willemia_koreana)),((Willemia_virae,(Willemia_unispina,Willemia_psammo
phila)
),(Willemia_bedosae,(Willemia_iztaccihuatlensis,Willemai_tali))))))
,(Willemia_intermedia,(Willemia_shanghaiensis,(Willemia_granulata
,(((Willemia_fjellbergi,Willemia_arida),(Willemia_trisphaerae
,(Willemia_elisabethum,Willemia_denisi))),(Willemia_japonica
,(Willemia_subbulbosa,(((Willemia_persimilis,Willemia_acantha)
,(Willemia_bulbosa,(Willemia_meybholae,Willemia_arenicola)))
,((Willemia_nepalensis,(Willemia_neocaledonica,(Willemia_nadchatrami
,Willemia_brevispina))),(Willemia_annapurna,(Willemia_buddenbrocki
,(Willemia_wandae,(Willemia_nosyboraha,(Willemia_delamarei
,(Willemia_setonychia,Willemia_deharvengi))))))))))))))))[154.];
(Hypogastrura_vernalis,(Orogastrura_dilatata,(Xenyllogastrura_octoculat
a
,((Willemia_multilobata,Willemia_bellingeri),((Willemia_trilobata
,Willemia_namibiae),((Willemia_similis,(Willemia_christianseni
,(Willemia_anophthalma,(Willemia_dubia,((Willemia_scandinavica
,Willemia_koreana),((Willemia_unispina,Willemia_psammophila)
,(Willemia_bedosae,(Willemia_iztaccihuatlensis,(Willemia_virae,Willemai
_tali)
))))))),(Willemia_intermedia,(Willemia_shanghaiensis,(Willemia_granula
ta
,((Willemia_fjellbergi,(Willemia_arida,(Willemia_trisphaerae
,(Willemia_elisabethum,Willemia_denisi)))),(Willemia_japonica
,(Willemia_subbulbosa,(((Willemia_persimilis,Willemia_acantha)
,(Willemia_bulbosa,(Willemia_meybholae,Willemia_arenicola)))
,((Willemia_nepalensis,((Willemia_nosyboraha,Willemia_delamarei)
,(Willemia_setonychia,Willemia_deharvengi))),(Willemia_annapurna
,(Willemia_buddenbrocki,(Willemia_wandae,(Willemia_neocaledonica
,(Willemia_nadchatrami,Willemia_brevispina))))))))))))))))[154.];
(Hypogastrura_vernalis,(Orogastrura_dilatata,(Xenyllogastrura_octoculat
a
,((Willemia_multilobata,Willemia_bellingeri),((Willemia_trilobata
,Willemia_namibiae),((Willemia_similis,(Willemia_christianseni
```

```
,(Willemia_anophthalma,((Willemia_scandinavica,Willemia_koreana)
,(Willemia_dubia,((Willemia_unispina,Willemia_psammophila),(Willemia_vi
rae
,(Willemia_bedosae,(Willemia_iztaccihuatlensis,Willemai_tali)))))))))
,(Willemia_intermedia,(Willemia_shanghaiensis,(Willemia_granulata
,(((Willemia_fjellbergi,Willemia_arida),(Willemia_trisphaerae
,(Willemia_elisabethum,Willemia_denisi))),(Willemia_japonica
,(Willemia_subbulbosa,(((Willemia_persimilis,Willemia_acantha)
,(Willemia_bulbosa,(Willemia_meybholae,Willemia_arenicola)))
,((Willemia_nepalensis,((Willemia_nosyboraha,Willemia_delamarei)
,(Willemia_setonychia,Willemia_deharvengi))),(Willemia_annapurna
,(Willemia_buddenbrocki,(Willemia_wandae,(Willemia_neocaledonica
,(Willemia_nadchatrami,Willemia_brevispina))))))))))))))))))[154.];
(Hypogastrura_vernalis,(Orogastrura_dilatata,(Xenyllogastrura_octoculat
a
,((Willemia_multilobata,Willemia_bellingeri),((Willemia_trilobata
,Willemia_namibiae),((Willemia_similis,(Willemia_christianseni
,(Willemia_anophthalma,((Willemia_scandinavica,Willemia_koreana)
,(Willemia_dubia,(Willemia_virae,((Willemia_iztaccihuatlensis
,Willemia_bedosae),(Willemai_tali,(Willemia_unispina,Willemia_psammophi
la))))
)))))),(Willemia_intermedia,(Willemia_shanghaiensis,(Willemia_granulata
,((Willemia_fjellbergi,(Willemia_arida,(Willemia_trisphaerae
,(Willemia_elisabethum,Willemia_denisi)))),(Willemia_japonica
,(Willemia_subbulbosa,(((Willemia_persimilis,Willemia_acantha)
,(Willemia_bulbosa,(Willemia_meybholae,Willemia_arenicola)))
,((Willemia_nepalensis,(Willemia_neocaledonica,(Willemia_nadchatrami
,Willemia_brevispina))),(Willemia_annapurna,(Willemia_buddenbrocki
,(Willemia_wandae,(Willemia_nosyboraha,(Willemia_delamarei
,(Willemia_setonychia,Willemia_deharvengi))))))))))))))))[154.];
(Hypogastrura_vernalis,(Orogastrura_dilatata,(Xenyllogastrura_octoculat
a
,((Willemia_multilobata,Willemia_bellingeri),((Willemia_trilobata
,Willemia_namibiae),((Willemia_similis,(Willemia_christianseni
,(Willemia_anophthalma,(Willemia_dubia,((Willemia_scandinavica
,Willemia_koreana),((Willemia_iztaccihuatlensis,Willemia_bedosae)
,(Willemia_virae,(Willemai_tali,(Willemia_unispina,Willemia_psammophila
))))))
))),(Willemia_intermedia,(Willemia_shanghaiensis,(Willemia_granulata
,((Willemia_fjellbergi,(Willemia_arida,(Willemia_trisphaerae
,(Willemia_elisabethum,Willemia_denisi)))),(Willemia_japonica
,(Willemia_subbulbosa,(((Willemia_persimilis,Willemia_acantha)
,(Willemia_bulbosa,(Willemia_meybholae,Willemia_arenicola)))
,((Willemia_nepalensis,((Willemia_nosyboraha,Willemia_delamarei)
,(Willemia_setonychia,Willemia_deharvengi))),(Willemia_annapurna
,(Willemia_buddenbrocki,(Willemia_wandae,(Willemia_neocaledonica
,(Willemia_nadchatrami,Willemia_brevispina))))))))))))))))))[154.];
```

will_results.ss is the data matrix with the resulting optimal trees readable by Winclada (obtained by the will_results.sh script run in POY):

```
xread 'Generated by POY 4.0' 52 45
Willemia_wandae 10030031111131111121001331110001101111111111111111101
Willemia_virae 10000001100010110101000111010001101111001?000100001
Willemia_trisphaerae
13112211100100l1?10100011101000110000110110101100011
Willemia_trilobata 00000001100110110l0?10023100000100110100001?1001???01
Willemai_tali 1111?01110001011010100011111000110111100110000110001
Willemia_subbulbosa
12222221111120110101000231010001100101101101001110O1
Willemia_similis 10000001100110110101000111010000100101000100001000100001
Willemia_shanghaiensis
100022011????????101000??100000110000??011????1??001
Willemia_setonychia
20030031l????111013l0????111110110111111l????1???11
Willemia_scandinavica
10002201100010110101000111O?000110110100001000010000l
Willemia_acantha 03002201l1?120110121010??10100111011111101101001110l1
Willemia_bulbosa
0322222111?1201101[01]1010??10100111011111011010011100l
Willemia_psammophila
00000001110010110111000331111101000101?01100001?0001
Willemia_persimilis
03002201l1?120110121010??10100111011111011010011100l
Willemia_nepalensis
10030031111131110121001221110001101111111011111110l
Willemia_neocaledonica
100300311111311111210012210100011011111111111111101
Willemia_namibiae 00000001100110110l0?1?023100000100110100001?100100?01
Willemia_nadchatrami
1003003111113111110100122100000110111l1?0111111??101
Willemia_multilobata
000002011001O0??0101000111000000000000000010100100001
Willemia_meybholae 022222211111211101310102310000111111111l0110100111011
Willemia_koreana 10002201100010110101000111010001101101000l0000100001
Willemia_japonica 100222211001001101010001110100011001011011010010001l
Willemia_iztaccihuatlensis
11000001100010110101000[12][12]10100111011O1?01100?0100001
Willemia_intermedia
13000001100100110101000111010001100001101101001000O1
Willemia_granulata 10002201100100110101000111010001100001101101001000l1
Willemia_unispina 100000001??10011?10100011111110110110100110000l??011
Willemia_fjellbergi
13322221100100110101000111010001100001101l?1?1100011
Willemia_elisabethum
11112111100100111101010111010011101111101101011000l1
Willemia_dubia 10000001100010110101000111010001101101000l0000100001
Willemia_denisi 11111111100100111101010111010011101111101101011000l1
Willemia_delamarei 100300311????111012100l??11111011011111111????1???01
Willemia_deharvengi
20030031111131110131001231111101101111111101111111l1
Willemia_christianseni
13000001100010110101000111010001100101000l0000100001
Willemia_buddenbrocki
10030031111131111121001331010001101111111101111111O1
```

```
Willemia_brevispina
13032031111131111101001221010001101111111111111111101
Willemia_bellingeri
00000201100100110101000111000000000000000010100100001
Willemia_bedosae 10000001100010110101000111010001101101001100000100001
Willemia_arida 1332222110?100110101000??10100011000011011010110011
Willemia_nosyboraha
10030031111??11111110013311111011011111111110010????01
Willemia_arenicola 022222211110211101210102310000111111111011010011100 1
Willemia_anophthalma
10000001100010110101000111010001000101000100000100001
Willemia_annapurna 10030031111131110131001331010001101111111101111111101
Xenyllogastrura_octoculata
00000001000?0100000001011000000000000010010?1000?0000
Orogastrura_dilatata
00000000000000000000000000000000000001010001010000??000
Hypogastrura_vernalis
000000000?000000000000000000000000000010???000000
;
cc - 0.51;
;
proc /;
#
$
;
cn {0 willemia2011.ss:0 A B C D E F G H I J K L M N O P Q R S T U V 0 1
2 3 4 5 6 7 8 9 ;
{1 willemia2011.ss:1 A B C D E F G H I J K L M N O P Q R S T U V 0 1 2
3 4 5 6 7 8 9 ;
{2 willemia2011.ss:2 A B C D E F G H I J K L M N O P Q R S T U V 0 1 2
3 4 5 6 7 8 9 ;
{3 willemia2011.ss:3 A B C D E F G H I J K L M N O P Q R S T U V 0 1 2
3 4 5 6 7 8 9 ;
{4 willemia2011.ss:4 A B C D E F G H I J K L M N O P Q R S T U V 0 1 2
3 4 5 6 7 8 9 ;
{5 willemia2011.ss:5 A B C D E F G H I J K L M N O P Q R S T U V 0 1 2
3 4 5 6 7 8 9 ;
{6 willemia2011.ss:6 A B C D E F G H I J K L M N O P Q R S T U V 0 1 2
3 4 5 6 7 8 9 ;
{7 willemia2011.ss:7 A B C D E F G H I J K L M N O P Q R S T U V 0 1 2
3 4 5 6 7 8 9 ;
{8 willemia2011.ss:8 A B C D E F G H I J K L M N O P Q R S T U V 0 1 2
3 4 5 6 7 8 9 ;
{9 willemia2011.ss:9 A B C D E F G H I J K L M N O P Q R S T U V 0 1 2
3 4 5 6 7 8 9 ;
{10 willemia2011.ss:10 A B C D E F G H I J K L M N O P Q R S T U V 0 1
2 3 4 5 6 7 8 9 ;
{11 willemia2011.ss:11 A B C D E F G H I J K L M N O P Q R S T U V 0 1
2 3 4 5 6 7 8 9 ;
{12 willemia2011.ss:12 A B C D E F G H I J K L M N O P Q R S T U V 0 1
2 3 4 5 6 7 8 9 ;
{13 willemia2011.ss:13 A B C D E F G H I J K L M N O P Q R S T U V 0 1
2 3 4 5 6 7 8 9 ;
{14 willemia2011.ss:14 A B C D E F G H I J K L M N O P Q R S T U V 0 1
2 3 4 5 6 7 8 9 ;
{15 willemia2011.ss:15 A B C D E F G H I J K L M N O P Q R S T U V 0 1
2 3 4 5 6 7 8 9 ;
```

```
{16 willemia2011.ss:16 A B C D E F G H I J K L M N O P Q R S T U V 0 1
2 3 4 5 6 7 8 9 ;
{17 willemia2011.ss:17 A B C D E F G H I J K L M N O P Q R S T U V 0 1
2 3 4 5 6 7 8 9 ;
{18 willemia2011.ss:18 A B C D E F G H I J K L M N O P Q R S T U V 0 1
2 3 4 5 6 7 8 9 ;
{19 willemia2011.ss:19 A B C D E F G H I J K L M N O P Q R S T U V 0 1
2 3 4 5 6 7 8 9 ;
{20 willemia2011.ss:20 A B C D E F G H I J K L M N O P Q R S T U V 0 1
2 3 4 5 6 7 8 9 ;
{21 willemia2011.ss:21 A B C D E F G H I J K L M N O P Q R S T U V 0 1
2 3 4 5 6 7 8 9 ;
{22 willemia2011.ss:22 A B C D E F G H I J K L M N O P Q R S T U V 0 1
2 3 4 5 6 7 8 9 ;
{23 willemia2011.ss:23 A B C D E F G H I J K L M N O P Q R S T U V 0 1
2 3 4 5 6 7 8 9 ;
{24 willemia2011.ss:24 A B C D E F G H I J K L M N O P Q R S T U V 0 1
2 3 4 5 6 7 8 9 ;
{25 willemia2011.ss:25 A B C D E F G H I J K L M N O P Q R S T U V 0 1
2 3 4 5 6 7 8 9 ;
{26 willemia2011.ss:26 A B C D E F G H I J K L M N O P Q R S T U V 0 1
2 3 4 5 6 7 8 9 ;
{27 willemia2011.ss:27 A B C D E F G H I J K L M N O P Q R S T U V 0 1
2 3 4 5 6 7 8 9 ;
{28 willemia2011.ss:28 A B C D E F G H I J K L M N O P Q R S T U V 0 1
2 3 4 5 6 7 8 9 ;
{29 willemia2011.ss:29 A B C D E F G H I J K L M N O P Q R S T U V 0 1
2 3 4 5 6 7 8 9 ;
{30 willemia2011.ss:30 A B C D E F G H I J K L M N O P Q R S T U V 0 1
2 3 4 5 6 7 8 9 ;
{31 willemia2011.ss:31 A B C D E F G H I J K L M N O P Q R S T U V 0 1
2 3 4 5 6 7 8 9 ;
{32 willemia2011.ss:32 A B C D E F G H I J K L M N O P Q R S T U V 0 1
2 3 4 5 6 7 8 9 ;
{33 willemia2011.ss:33 A B C D E F G H I J K L M N O P Q R S T U V 0 1
2 3 4 5 6 7 8 9 ;
{34 willemia2011.ss:34 A B C D E F G H I J K L M N O P Q R S T U V 0 1
2 3 4 5 6 7 8 9 ;
{35 willemia2011.ss:35 A B C D E F G H I J K L M N O P Q R S T U V 0 1
2 3 4 5 6 7 8 9 ;
{36 willemia2011.ss:36 A B C D E F G H I J K L M N O P Q R S T U V 0 1
2 3 4 5 6 7 8 9 ;
{37 willemia2011.ss:37 A B C D E F G H I J K L M N O P Q R S T U V 0 1
2 3 4 5 6 7 8 9 ;
{38 willemia2011.ss:38 A B C D E F G H I J K L M N O P Q R S T U V 0 1
2 3 4 5 6 7 8 9 ;
{39 willemia2011.ss:39 A B C D E F G H I J K L M N O P Q R S T U V 0 1
2 3 4 5 6 7 8 9 ;
{40 willemia2011.ss:40 A B C D E F G H I J K L M N O P Q R S T U V 0 1
2 3 4 5 6 7 8 9 ;
{41 willemia2011.ss:41 A B C D E F G H I J K L M N O P Q R S T U V 0 1
2 3 4 5 6 7 8 9 ;
{42 willemia2011.ss:42 A B C D E F G H I J K L M N O P Q R S T U V 0 1
2 3 4 5 6 7 8 9 ;
{43 willemia2011.ss:43 A B C D E F G H I J K L M N O P Q R S T U V 0 1
2 3 4 5 6 7 8 9 ;
{44 willemia2011.ss:44 A B C D E F G H I J K L M N O P Q R S T U V 0 1
2 3 4 5 6 7 8 9 ;
```

```
{45 willemia2011.ss:45 A B C D E F G H I J K L M N O P Q R S T U V 0 1
2 3 4 5 6 7 8 9 ;
{46 willemia2011.ss:46 A B C D E F G H I J K L M N O P Q R S T U V 0 1
2 3 4 5 6 7 8 9 ;
{47 willemia2011.ss:47 A B C D E F G H I J K L M N O P Q R S T U V 0 1
2 3 4 5 6 7 8 9 ;
{48 willemia2011.ss:48 A B C D E F G H I J K L M N O P Q R S T U V 0 1
2 3 4 5 6 7 8 9 ;
{49 willemia2011.ss:49 A B C D E F G H I J K L M N O P Q R S T U V 0 1
2 3 4 5 6 7 8 9 ;
{50 willemia2011.ss:50 A B C D E F G H I J K L M N O P Q R S T U V 0 1
2 3 4 5 6 7 8 9 ;
{51 willemia2011.ss:51 A B C D E F G H I J K L M N O P Q R S T U V 0 1
2 3 4 5 6 7 8 9 ;
;

tread (Hypogastrura_vernalis (Orogastrura_dilatata
(Xenyllogastrura_octoculata ((Willemia_multilobata Willemia_bellingeri)
((Willemia_trilobata Willemia_namibiae) ((Willemia_similis
((Willemia_christianseni Willemia_anophthalma) ((Willemia_dubia
(Willemia_scandinavica Willemia_koreana)) (Willemia_iztaccihuatlensis
(Willemia_bedosae ((Willemia_unispina Willemia_psammophila)
(Willemia_virae Willemai_tali))))))) (Willemia_intermedia
(Willemia_shanghaiensis (Willemia_granulata (((Willemia_fjellbergi
Willemia_arida) (Willemia_trisphaerae (Willemia_elisabethum
Willemia_denisi))) (Willemia_japonica (Willemia_subbulbosa
(((Willemia_persimilis Willemia_acantha) (Willemia_bulbosa
(Willemia_meybholae Willemia_arenicola))) ((Willemia_nepalensis
(Willemia_neocaledonica (Willemia_nadchatrami Willemia_brevispina)))
(Willemia_annapurna (Willemia_buddenbrocki (Willemia_wandae
(Willemia_nosyboraha (Willemia_delamarei (Willemia_setonychia
Willemia_deharvengi)))))))))))))))) * (Hypogastrura_vernalis
(Orogastrura_dilatata (Xenyllogastrura_octoculata
((Willemia_multilobata Willemia_bellingeri) ((Willemia_trilobata
Willemia_namibiae) ((Willemia_similis ((Willemia_christianseni
Willemia_anophthalma) ((Willemia_dubia (Willemia_scandinavica
Willemia_koreana)) ((Willemia_virae (Willemia_unispina
Willemia_psammophila)) (Willemia_bedosae (Willemia_iztaccihuatlensis
Willemai_tali)))))) (Willemia_intermedia (Willemia_shanghaiensis
(Willemia_granulata (((Willemia_fjellbergi Willemia_arida)
(Willemia_trisphaerae (Willemia_elisabethum Willemia_denisi)))
(Willemia_japonica (Willemia_subbulbosa (((Willemia_persimilis
Willemia_acantha) (Willemia_bulbosa (Willemia_meybholae
Willemia_arenicola))) ((Willemia_nepalensis (Willemia_neocaledonica
(Willemia_nadchatrami Willemia_brevispina))) (Willemia_annapurna
(Willemia_buddenbrocki (Willemia_wandae (Willemia_nosyboraha
(Willemia_delamarei (Willemia_setonychia
Willemia_deharvengi)))))))))))))))) * (Hypogastrura_vernalis
(Orogastrura_dilatata (Xenyllogastrura_octoculata
((Willemia_multilobata Willemia_bellingeri) ((Willemia_trilobata
Willemia_namibiae) ((Willemia_similis (Willemia_christianseni
(Willemia_anophthalma (Willemia_dubia ((Willemia_scandinavica
Willemia_koreana) ((Willemia_unispina Willemia_psammophila)
(Willemia_bedosae (Willemia_iztaccihuatlensis (Willemia_virae
Willemai_tali)))))))) (Willemia_intermedia (Willemia_shanghaiensis
(Willemia_granulata ((Willemia_fjellbergi (Willemia_arida
(Willemia_trisphaerae (Willemia_elisabethum Willemia_denisi))))
(Willemia_japonica (Willemia_subbulbosa (((Willemia_persimilis
```

```
Willemia_acantha) (Willemia_bulbosa (Willemia_meybholae
Willemia_arenicola))) ((Willemia_nepalensis ((Willemia_nosyboraha
Willemia_delamarei) (Willemia_setonychia Willemia_deharvengi)))
(Willemia_annapurna (Willemia_buddenbrocki (Willemia_wandae
(Willemia_neocaledonica (Willemia_nadchatrami
Willemia_brevispina)))))))))))))))) * (Hypogastrura_vernalis
(Orogastrura_dilatata (Xenyllogastrura_octoculata
((Willemia_multilobata Willemia_bellingeri) ((Willemia_trilobata
Willemia_namibiae) ((Willemia_similis (Willemia_christianseni
(Willemia_anophthalma ((Willemia_scandinavica Willemia_koreana)
(Willemia_dubia ((Willemia_unispina Willemia_psammophila)
(Willemia_virae (Willemia_bedosae (Willemia_iztaccihuatlensis
Willemai_tali)))))))) (Willemia_intermedia (Willemia_shanghaiensis
(Willemia_granulata (((Willemia_fjellbergi Willemia_arida)
(Willemia_trisphaerae (Willemia_elisabethum Willemia_denisi)))
(Willemia_japonica (Willemia_subbulbosa (((Willemia_persimilis
Willemia_acantha) (Willemia_bulbosa (Willemia_meybholae
Willemia_arenicola))) ((Willemia_nepalensis ((Willemia_nosyboraha
Willemia_delamarei) (Willemia_setonychia Willemia_deharvengi)))
(Willemia_annapurna (Willemia_buddenbrocki (Willemia_wandae
(Willemia_neocaledonica (Willemia_nadchatrami
Willemia_brevispina)))))))))))))))) * (Hypogastrura_vernalis
(Orogastrura_dilatata (Xenyllogastrura_octoculata
((Willemia_multilobata Willemia_bellingeri) ((Willemia_trilobata
Willemia_namibiae) ((Willemia_similis (Willemia_christianseni
(Willemia_anophthalma ((Willemia_scandinavica Willemia_koreana)
(Willemia_dubia (Willemia_virae ((Willemia_iztaccihuatlensis
Willemia_bedosae) (Willemai_tali (Willemia_unispina
Willemia_psammophila)))))))) (Willemia_intermedia
(Willemia_shanghaiensis (Willemia_granulata ((Willemia_fjellbergi
(Willemia_arida (Willemia_trisphaerae (Willemia_elisabethum
Willemia_denisi)))) (Willemia_japonica (Willemia_subbulbosa
(((Willemia_persimilis Willemia_acantha) (Willemia_bulbosa
(Willemia_meybholae Willemia_arenicola))) ((Willemia_nepalensis
(Willemia_neocaledonica (Willemia_nadchatrami Willemia_brevispina)))
(Willemia_annapurna (Willemia_buddenbrocki (Willemia_wandae
(Willemia_nosyboraha (Willemia_delamarei (Willemia_setonychia
Willemia_deharvengi)))))))))))))))) * (Hypogastrura_vernalis
(Orogastrura_dilatata (Xenyllogastrura_octoculata
((Willemia_multilobata Willemia_bellingeri) ((Willemia_trilobata
Willemia_namibiae) ((Willemia_similis (Willemia_christianseni
(Willemia_anophthalma (Willemia_dubia ((Willemia_scandinavica
Willemia_koreana) ((Willemia_iztaccihuatlensis Willemia_bedosae)
(Willemia_virae (Willemai_tali (Willemia_unispina
Willemia_psammophila)))))))) (Willemia_intermedia
(Willemia_shanghaiensis (Willemia_granulata ((Willemia_fjellbergi
(Willemia_arida (Willemia_trisphaerae (Willemia_elisabethum
Willemia_denisi)))) (Willemia_japonica (Willemia_subbulbosa
(((Willemia_persimilis Willemia_acantha) (Willemia_bulbosa
(Willemia_meybholae Willemia_arenicola))) ((Willemia_nepalensis
((Willemia_nosyboraha Willemia_delamarei) (Willemia_setonychia
Willemia_deharvengi))) (Willemia_annapurna (Willemia_buddenbrocki
(Willemia_wandae (Willemia_neocaledonica (Willemia_nadchatrami
Willemia_brevispina)))))))))))))))));
```

bremer_w.sh and jackknife_w.sh are the scripts for bremer and jackknife calcultion respectively; will-one.tre file contains one of the six optimal tree for the purpose of these calculations;

bremer_w.sh:

```
wipe ()
read ("willemia2011.ss")
set (root: "Hypogastrura_vernalis")
read ("willone.tre")
report ("bremerw.txt", supports:bremer:"will-bre1.trees")
report ("bremerw", graphsupports:bremer:"will-bre1.trees")
exit ()
```

jackknife_w.sh:

```
wipe ()
read ("willemia2011.ss")
set (root: "Hypogastrura_vernalis")
read ("will-one.tre")
calculate_support(jackknife:(remove:0.50, resample:1000), build(),
swap(tbr, trees:5))
report ("jackknife_w", graphsupports:jackknife)
exit ()
```

will-one.tre:

```
(Hypogastrura_vernalis,(Orogastrura_dilatata,(Xenyllogastrura_octoculat
a
,((Willemia_multilobata,Willemia_bellingeri),((Willemia_trilobata
,Willemia_namibiae),((Willemia_similis,((Willemia_christianseni
,Willemia_anophthalma),((Willemia_dubia,(Willemia_scandinavica
,Willemia_koreana)),(Willemia_iztaccihuatlensis,(Willemia_bedosae
,((Willemia_unispina,Willemia_psammophila),(Willemia_virae,Willemai_tal
i)))))
)),(Willemia_intermedia,(Willemia_shanghaiensis,(Willemia_granulata
,(((Willemia_fjellbergi,Willemia_arida),(Willemia_trisphaerae
,(Willemia_elisabethum,Willemia_denisi))),(Willemia_japonica
,(Willemia_subbulbosa,(((Willemia_persimilis,Willemia_acantha)
,(Willemia_bulbosa,(Willemia_meybholae,Willemia_arenicola)))
,((Willemia_nepalensis,(Willemia_neocaledonica,(Willemia_nadchatrami
,Willemia_brevispina))),(Willemia_annapurna,(Willemia_buddenbrocki
,(Willemia_wandae,(Willemia_nosyboraha,(Willemia_delamarei
,(Willemia_setonychia,Willemia_deharvengi))))))))))))))))))[154.];
```

Appendix S1d: Willemia phylogeny and characters: results

Figure Appendix S1 shows the strict consensus of 6 most parsimonious trees with a tree length of 154 steps, with jacknife and Bremer indices indicated at each node. Consistency Index is 46 and Retention Index is 82. All trees, jackknife, statistics and Bremer supports can be found in Electronic Appendix S1c. The addition of the 5 new *Willemia* species did not change the general topology found in D'Haese (2000). The monophyly of the genus *Willemia* was confirmed and strongly supported (jackknife resampling percentage of 100% and Bremer support value 3). The *anophthalma*, *denisi* s.str. and *buddenbrocki* groups were retrieved monophyletic again and the *denisi* group *sensu* Potapov is still paraphyletic (with the addition of *W. shanghaiensis* between *W. intermedia* and *W. granulata* in a paraphyletic assemblage). The new species (for the analysis) W. *tali, W. iztaccihuatlensis, W. psammophila* and *W. unispina* belong to the *anophthalma* group. *W. acantha* is sister group to *W. persimilis*, in the same group, *W. bulbosa* is sister group to *W. arenicola + W. meybholae*. Lastly, *W. nosyboraha* is included in the *buddenbrocki* group. Table 1 and Table in Appendix S2e show biogeographic and ecological attributes of species, respectively. In these tables species were arranged in the order given by the phylogeny.

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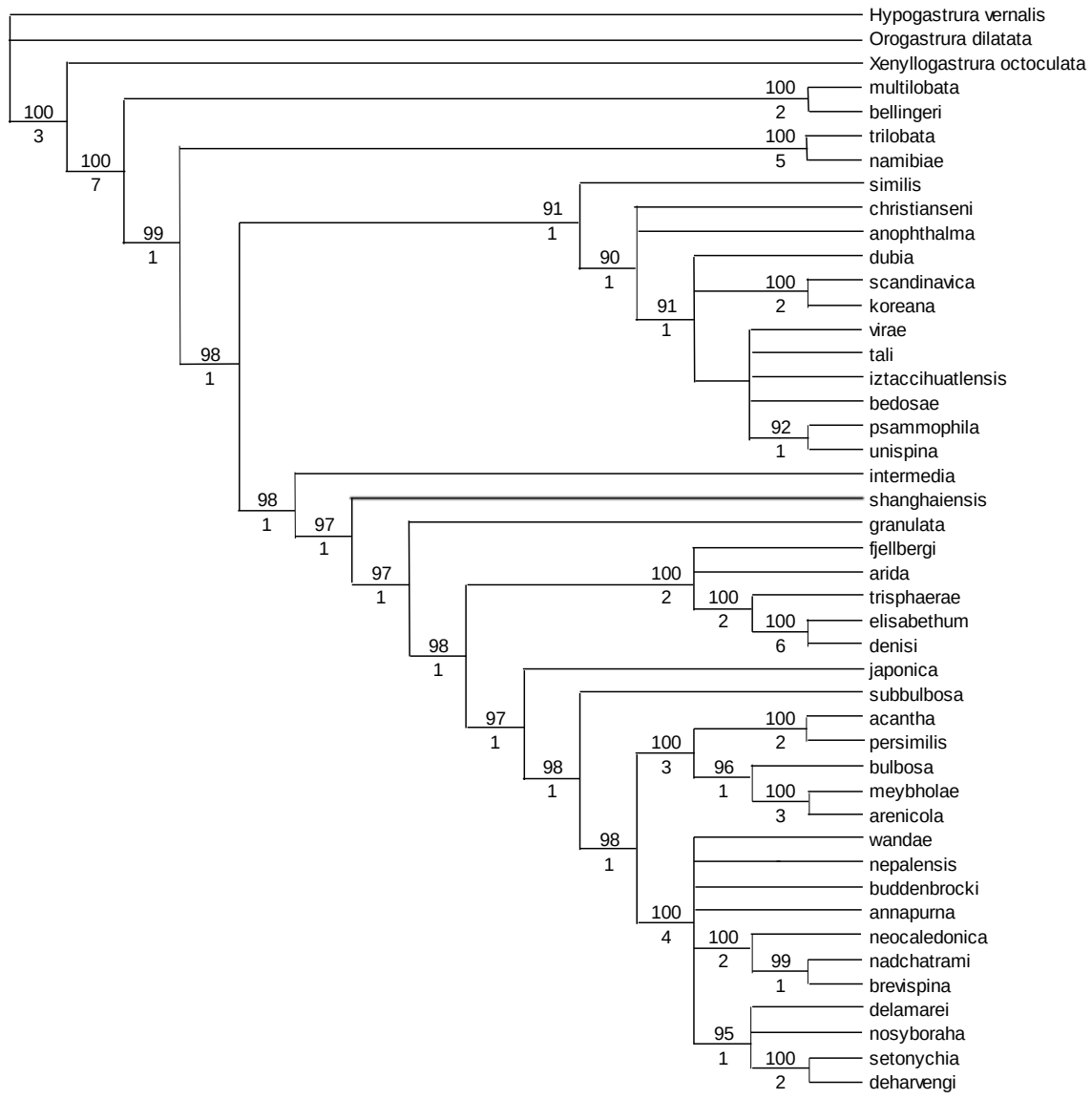
D'Haese, C. (2000) Is psammophily an evolutionary dead end? A phylogenetic test in the genus Willemia (Collembola: Hypogastruridae). *Cladistics*, **16**, 255–273.

Figure Appendix S1. Strict majority consensus of six phylogenetic trees of the genus *Willemia*, with three outgroup species (see text for more details). Jacknife resampling percentages and Bremer support values are indicated above and below each node, respectively.



Appendix S2: Literature research: definitions, references, exploration of biases

Appendix S2a – Definitions of factors of harshness

- ‘xeric’ was defined as an environment displaying permanent or seasonal aridity: deserts (whether warm or cold), matorrals, sand dunes with poor vegetation cover, karst landscapes and dry Mediterranean areas

- ‘hydric’ was defined as an environment displaying excess of water and associated lack of soil atmosphere: waterlogged soils, flooded areas

- ‘arctic’ was defined as an environment displaying a long period of frost, generally more than six months, reflecting a latitudinal temperature gradient: polar, arctic and subarctic environments

- ‘alpine’ was defined as an environment displaying a long period of frost, generally more than six months, reflecting an altitudinal temperature gradients: high mountains, including alpine and subalpine climates, above 1,000 m in nordic countries, above 2,000 m in temperate areas, above 3,000 or 4,000 m in tropical areas

- ‘acid’ was defined as a soil at pH_{water} less than 5, where free aluminium and high phenolic concentrations are likely to occur: raw humus, podzols

- ‘metallic’ was defined as a soil polluted with heavy metals: areas in the vicinity of smelter or mining activities

- ‘saline’ was defined as a soil with a high osmotic pressure due to a high charge in salts (beaches and salt deserts).

Every species could be assigned to several harsh habitats according to (*i*) multiple records of the same species in a variety of habitats, or (*ii*) habitats belonging to several harshness

categories. For instance, over the whole array of literature consulted, the same species can be recorded both in waterlogged and arid soils or the same habitat can be ‘arctic’ and ‘acid’, but only when this was indicated. In our census we did not try to discern whether some factors were dominant above others in a given record unit. Rather we considered them as independent causes of harshness, with which species must cope within a given habitat throughout their evolutionary history (Jablonski, 2008).

Caves were excluded given that (*i*) they constitute refuges where more sensitive species can live in a more buffered environment, whatever the nature of the surrounding environment, (*ii*) there was no evidence they were detrimental to growth and reproduction of most soil invertebrate species (Moseley, 2007), and (*iii*) some *Willemia* species were reported to occur in caves (some of them were even described for the first time in caves) but they were also found in other environments, suggesting the absence of specialisation for cave life in this genus (Christiansen, 1965). Psammophily sensu D’Haese (2000), i.e. life in sand, was partitioned in ‘saline’ and ‘xeric’ categories according to whether sea water or drought was the prevailing factor. For instance seashore dunes were considered ‘xeric’ but not ‘saline’ while the intertidal zone was considered ‘saline’ but not ‘xeric’. Experimental studies focusing on individual *Willemia* species as well as on entire soil communities were also taken into account. The ‘harshness breadth’ index was estimated for every species by the number of harsh environments in which the species was recorded, thus scaling from 0 (no harsh environment recorded for the species) to 7 (all harsh environments recorded).

Obviously, no place on earth will show all types of harshness. This is why we considered multiple types of harshness, and why we quantified the harshness breadth as the number of harshness types occupied by a given species. Moreover, we tested whether occupation of different types of harshness is positively or negatively correlated, i.e. whether species that can tolerate certain kinds of harsh environments tend to be able to tolerate a broad

range of harsh environments (except those affected by salinity). We found that occupations of all but one type of harshness are positively correlated (Results). This means that a species that is found in environments that are harsh in one type tend to be found under different types of harsh environments, too. Inversely, other species occupy environments lacking any of the types of harshness. This result justifies talking broadly about "species using harsh environments" as we repeatedly do it.

The largest possible corpus of literature was examined for the assessment of use of harsh environments in *Willemia* species. As defined above (Introduction), harsh environments are those which limit the rate of growth and reproduction of most species, except a few ones tolerating it. This does not mean that harsh environments are poorer in Collembolan individuals, since better adapted species may benefit from the alleviation of competition caused by the resulting decrease in species richness and thereby may locally proliferate (Usher, 1985). A total of 248 references were used for the census (Appendix S2b). Languages available to us were English, French, German, Italian, Portugese and Spanish, embracing most literature published in books and scientific journals. Other languages (Russian, Japanese, Hungarian) were cautiously discarded, in order to avoid misinterpretation, but they comprised less than 1% of published literature. When information about soil or climate was not given for a record, but the plant community was sufficiently described in the vicinity of the sample, then vegetation was used as a basis for estimating the harshness of the environment: in several instances dominant ericaceous or coniferous vegetation was considered as indicative of soil acidity given the recalcitrance of its litter and its known acidifying influence on the environment occupied by *Willemia* (Ponge, 2000), while grassland species were indicative of more fertile and less acid soils (Miles, 1985; Falkengren-Grerup, 1986). In two instances, the geographic locality was sufficiently precise and was used to derive environmental conditions

prevailing at the sampling site. In the absence of any clue on environmental conditions, records were disregarded.

The above classification might miss species that are able to use harsh environments but did not happen to encounter any. However, given that we accounted for a large range of harsh environments, species in all regions should have encountered at least some of them (and use of one kind of harsh environment turn out to be positively correlated to the use of all others in most cases, see Results). Not occurring in harsh environments is hence true evidence for not being able to use them.

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1998

1999 Appendix S2b - References used for the assessment of use of harsh environments in *Willemia*

2000 species.

2001

acantha	1	Bonet (1945)
annapurna	2	d'Haese & Weiner (1998), Thibaud (2004)
anophthalma	156	Handschin (1924), Marlier (1942), Gisin (1943, 1947), Weber (1950), Haybach (1959), Gisin (19 (1961), Cassagnau & Rapoport (1962), Hüther (1962), Agrell (1963), Petersen (1965), Hale (19 (1967), Stebaeva (1967), Nosek (1967), Rusek (1968), Usher (1970), Jahn (1972), Gough (197 (1973), Axelsson et al. (1973), Blackith (1974), Kaczmarek (1975a, b), Dunger (1975), Usher (1 (1976), Fjellberg (1976), Ryan (1977), Lohm et al. (1977), Persson & Lohm (1977), Loksa (1978 (1979), Petersen (1980), Ponge (1980), Hutson (1980a, b), Abrahamsen et al. (1980), Bååth et & Kjøndal (1981a, b), Izarra (1981), Hågvar (1982), Ponge & Prat (1982), Huhta et al. (1983), G (1983), Ponge (1983), Hågvar (1983, 1984a, b), Hågvar & Abrahamsen (1984), Poursin & Pong al. (1984), Axelsson et al. (1984), Fjellberg (1984, 1985), Arbea & Jordana (1985a, 1986), Fjellb et al. (1986), Pozo (1986), Ardanaz & Jordana (1986), Poinsot-Balaguer & Tabone (1986), Pozo Huhta et al. (1986), Vilkamaa & Huhta (1986), Bolger (1986), Ponge et al. (1986), Kuznetsova (& Greven (1987), Hågvar (1987), Melecis (1987), Bengtsson & Rundgren (1988), Fjellberg (198 (1988), Pichard et al. (1989), Arbea & Jordana (1989, 1990), Hågvar & Abrahamsen (1990), Ma (1991), Gerdsmeier & Greven (1992), Ponge (1993), Babenko (1994), Kopeszki & Meyer (1994) Trockner (1994), Hågvar (1994), Rusek (1994), Fjellberg (1994), Lauga-Reyrel & Lauga (1995), Deharveng & Lek (1995), Koehler et al. (1995), Salminen et al. (1995), Rusek (1996), Shaw & U Deharveng (1996), Kopeszki & Meyer (1996), Haimi & Siira-Pietikäinen (1996), Filser & Hölsche et al. (1997), Fjellberg (1998), Therrien et al. (1999), Traser (1999), Sławska (2000), Ponge (200 et al. (2000a, b, 2001a, b), Loranger et al. (2001), Ojala & Huhta (2001), Siira-Pietikäinen et al. (2002), Kuznetsova (2002), Pflug & Wolters (2002), Babenko (2002), Lek-Ang & Deharveng (20 Ponge (2002), Shrubovych (2002), Ponge et al. (2002, 2003), Chauvat et al. (2003), Stebaeva ((2003a, b), Gruia (2003), Cassagne et al. (2003, 2004), Lindberg & Persson (2004), Materna (2 (2004), Petersen et al. (2004), Garnier & Ponge (2004), Gillet & Ponge (2004), Dunger et al. (20 (2004), Lindberg & Bengtsson (2005), Kuznetsova (2006), Traser & Horváth-Szováti (2006), Hu Syrek et al. (2006), Ponge et al. (2006), Sleptzova & Reznikova (2006), Chauvat et al. (2007), J (2007), Hopkin (2007), Raschmanová et al. (2008), Salamon et al. (2008), Mordkovich et al. (20 (2008, 2009), Auclerc et al. (2009), Salamon & Alphei (2009), Sławska & Sławski (2009)
arenicola	2	Palacios-Vargas & Vázquez (1988), Palacios-Vargas & Thibaud (2001)
arida	2	Fjellberg (1991), Addison et al. (2006)
bedosae	3	d'Haese (1998), Thibaud (2004), Raschmanová et al. (2008)
bellingeri	1	Palacios-Vargas & Vázquez (1988)
brevispina	10	Hüther (1962), Rapoport (1962), Palacios-Vargas (1987), Najt et al. (1990), Christiansen & Belli Thibaud (1993), d'Haese & Weiner (1998), Thibaud & Palacios-Vargas (1999), Culik & Zeppelin al. (2006)
buddenbrocki	19	Hüther (1959, 1962), Rapoport & Rubio (1963), Gough (1972), Ponge (1983), Arpin et al. (1984 al. (1985), Fjellberg (1992), Ponge (1993), Sabatini et al. (1997), Jordana et al. (1997), Rebecch Ponge (2000a), Chauvat & Ponge (2002), Gómez-Anaya & Palacios-Vargas (2004), Thibaud (2 Ponge (2005), Hopkin (2007)
bulbosa	2	Bonet (1945), Cutz-Pool et al. (2007)
christianseni	1	d'Haese (1998)
deharvengi	1	d'Haese & Weiner (1998)
delamarei	1	Prabhoo (1971)
denisi	77	Gisin (1960), Cassagnau (1961), Hüther (1962), Petersen (1965), Szeptycki (1967), Nosek (196 Bödvarsson (1973), Axelsson et al. (1973), Fjellberg (1976), Bonnet et al. (1976, 1979), Hutson Lienhard (1980), Bååth et al. (1980), Ponge & Prat (1982), Hågvar (1982, 1983), Gers & Izarra (Kannowski (1984), Hågvar & Abrahamsen (1984), Axelsson et al. (1984), Fjellberg (1984, 1985) Jordana (1985b, 1986), Pozo et al. (1986), Bolger (1986), Kuznetsova (1987), Melecis (1987), E Rundgren (1988), Fjellberg (1988), Arbea & Jordana (1989), Gerdsmeier & Greven (1992), Batti (1993), Kopeszki & Meyer (1994), Kopeszki & Trockner (1994), Lopes & da Gama (1994), Deha (1995), Rusek & Marshall (1995), Rusek (1996), Deharveng (1996), Jordana et al. (1997), Fjellb

		(2000b), Ojala & Huhta (2001), Loranger et al. (2001), Chagnon et al. (2001b), Babenko (2002), (2002), Addison et al. (2003), Babenko (2003a, b), Ponge et al. (2003), Cassagne et al. (2003, 2 (2004), Garnier & Ponge (2004), Gillet & Ponge (2004), Koolhaas et al. (2004), Thibaud (2004), (2006), Syrek et al. (2006), Sørensen et al. (2006), Traser & Horváth-Szováti (2006), Addison et Chahartaghi et al. (2006), Ponge et al. (2006), Kuznetsova (2006, 2007), Chauvat et al. (2007), (2008), Babenko (2008), Raschmanová et al. (2008), Salamon & Alphei (2009), Auclerc et al. (2
dubia	3	Christiansen & Bellinger (1980), Benner & Kannowski (1984), d'Haese (1998)
elisabethum	1	Weiner (1986)
fjellbergi	3	Babenko (2003a, b), Thibaud (2004)
granulata	3	Fjellberg (1984, 1985), Addison et al. (2006)
intermedia	60	Mills (1934), Bellinger (1954), Hüther (1962), Wray et al. (1963), Szeptycki (1967), Gough (1972 Huhta et al. (1979), Lienhard (1980), Ponge & Prat (1982), Ponge (1983), Arpin et al. (1984), Po (1984), Arbea & Jordana (1986), Bolger (1986), Weiner (1986), Luciáñez Sánchez & Simón Ber (1988), Simón Benito & Pozo Martínez (1988), Fjellberg (1988), Sterzynska (1989), Arbea & Jor Rusek (1990), Zerling (1990), Sterzinska (1990), Palacios-Vargas (1990), Fjellberg (1992), Pong Battigelli & Marshall (1993), Kováč & Miklisová (1995), Rusek & Marshall (1995), Filser (1995), (1997), Jordana et al. (1997), da Gama et al. (1997, 1998), Fjellberg (1998), Barrocas et al. (199 (1999), Ponge (2000a), Loranger et al. (2001), Otrysko & Pagé (2001), Shrubovych (2002), Tras Stebaeva (2003), Addison et al. (2003), Ponge et al. (2003), Petersen et al. (2004), Dunger et a (2004), Kováč et al. (2005), Gillet & Ponge (2005), Traser & Horváth-Szováti (2006), Addison et et al. (2006), Sleptzova & Reznikova (2006), Debeljak et al. (2007), Hopkin (2007), Raschmanov Babenko (2008)
iztaccihuatlensis	2	García-Gómez & Cutz-Pool (2008), García-Gómez et al. (2009)
japonica	2	Tanaka & Kitazawa (1982), Thibaud (2004)
koreana	2	Thibaud & Lee (1994), Thibaud (2004)
meybholae	1	Palacios-Vargas (1987)
multilobata	8	Gers & Deharveng (1985), Fjellberg (1992, 1998), Babenko (2003a, b), Sterzynska & Bolger (20 (2004), Hopkin (2007)
nadchatrami	2	Yosii (1959), McClure et al. (1967)
namibiae	1	Thibaud & Massoud (1988)
neocaledonica	5	Weiner (1991), d'Haese & Weiner (1998), Thibaud (2002, 2009a, b)
nepalensis	2	d'Haese & Weiner (1998), Thibaud (2004)
nosyboraha	1	Thibaud (2008)
persimilis	6	Bonet (1945), Hüther (1962), Palacios-Vargas (1981), Palacios-Vargas & Gómez-Anaya (1993) Palacios-Vargas (2004), Cutz-Pool et al. (2007)
psammophila	1	Palacios-Vargas & Thibaud (2001)
scandinavica	34	Gisin (1947), Haybach (1959), Hüther (1962), Gough (1972), Dunger (1975), Fjellberg (1976, 19 & Jordana (1986), Fjellberg (1988, 1994), Babenko (1994), Hertzberg et al. (1994), Kováč (1994 Marshall (1995), Koehler et al. (1995), Sterzyńska & Ehrnsberger (1997), Jordana et al. (1997), Traser (1999), Babenko (2000), Shrubovych (2002), Traser (2002), Bondarenko-Borisova & San Babenko (2003a, b), Thibaud (2004), Kováč et al. (2005), Sørensen et al. (2006), Traser & Horv (2006), Arbea & MartÍnez Monteagudo (2006), Moseley (2007), Hopkin (2007), Raschmanová e
setonychia	1	Prabhoo (1971)
shanghaiensis	1	Yue (1999)
similis	20	Mills (1934), Weber (1950), Wray (1950), Wray et al. (1963), Benner & Kannowski (1984), Fjellb 1986, 1988), Rusek (1994), Babenko (1994), Fjellberg (1994, 1998), d'Haese (1998), Babenko (Thibaud (2004), Sørensen et al. (2006), Addison et al. (2006)
subbulbosa	1	Thibaud (1994)
tali	1	Kaprus' & Nevo (2003)
trilobata	1	Barra (1995)
trisphaerae	7	Babenko (2002), Stebaeva (2003), Babenko (2003a, b), Thibaud (2004), Babenko (2008, 2009)
unispina	1	Fjellberg (2007)
virae	5	Kaprus' (1997), Skarżyński & Smolis (2002), Thibaud (2004), Traser & Horváth-Szováti (2006), (2006)
wandae	3	Tamura & Zhao (1997), d'Haese & Weiner (1998), Thibaud (2004)

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Appendix S2c – Exploration of bias due to differences between species in numbers of records in the literature.

Methods: Because species differed in the number of records from which harshness-breadth was estimated (see above Appendix S2b, column 2), we also verified whether the number of records was 'phylogenetically conserved'. For this, we also used the root-skewness test with Euclidean distances among species. This test aims to highlight whether our results were biased by differences among species in the amount of knowledge on their environmental distribution. This approach is conservative: the intensive study of a species may increase the number of records in harsh environments (bias), but a species' use of harsh environments may also increase the chance of being observed in many of the environments studied (non-bias).

Results: There was no phylogenetic structure in the number of literature records (root-skewness test P-value = 0.326) even after log-transformation (root-skewness test P-value = 0.291) indicating that the analyses done in the main text on the link between phylogeny and properties of species do not depend on the extent to which these species were studied in the literature.

Appendix S2d: Salinity and tolerance to harshness.

We showed that in the genus *Willemia* tolerance to salinity (use of haline habitats) was negatively correlated to other types of harshness and that 'haline' species exhibited on average a higher clade rank than species tolerant of other harshness factors such as drought, frost, acidity, waterlogging (anaerobiosis) or heavy metals. In the absence of ecophysiological studies on the genus *Willemia*, which is probably explained by the small size of these animals and their concealed way of life (d'Haese, 2000), only putative arguments can be given for rejecting salinity as a harshness factor to which *Willemia* should adapt for life on the seashore. A strong attraction to sodium (compared to potassium) has been shown to occur in *Heteromurus nitidus*, another soil-dwelling springtail species (Salmon et al., 2002). Thibaud (2007), on the base of biogeographic arguments, postulated that transport by sea currents could be responsible for the occurrence of the same *Willemia* species on remote seashores, whether insular or continental. Witteveen *et al.* (1987) showed that the ionic concentration of the haemolymph of inland Collembola equilibrated rapidly with sea water when transferred to seashore conditions. It could be suggested that permanent contact with dilute saline solutions (seashores, but not dry saline environments) needs no special adaptation in basal Hexapoda, contrary to fully terrestrial insects (higher insects), for which potassium is an essential element which replaces sodium (Wigglesworth, 1965). The ancestry of life in sea water versus freshwater has been shown to be the rule in aquatic invertebrates (Lee & Bell, 1999). The separation we performed between tolerance to drought and to salinity, based on ecophysiological and biocenotic grounds (Hartmut *et al.*, 1995; Thibaud, 2007), and supported by studies on other animal groups (Gomez-Mestre & Tejedo, 2005), might explain why psammophily (life in sand), which confounds both adaptation to drought and to salinity, exhibits a high degree of reversal along phylogenetic trees of the genus *Willemia* (d'Haese, 2000).

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Appendix S2e: Identification and interpretation of biogeographic provinces.

The Gondwana (Antarctica, South America, Africa, Australasia, Madagascar, India and Himalaya, South-East Asia, Caribbean) or Laurasia (North America, Greenland, Europe, Asia except South-East Asia) origin of each biogeographic province was estimated from maps by McLoughlin (2001), except for Macaronesia (volcanic islands of North Atlantic) and Central America which did not exist at the time of Pangea disruption and the spread of present-day continents. Obviously, these two biogeographic distributions are strongly linked but they are not identical. While all 20 species from the former Laurasia domain are extra-tropical, only 8 of the 12 species from former Gondwana domain are tropical. In the latter analyses we only accounted for the 32 species which could be classified for both tropical/non-tropical and Gondwana/Laurasia distribution, permitting better comparability. Accounting for all species, however, lead to the same qualitative conclusions. We are aware of the fact that strong geographic discrepancies exist in the sampling effort devoted to Collembola (Deharveng, 2004). This is why we used the number of records per species (used as a proxy for sampling effort) to check for the absence of biases due to sampling imbalances (see Appendix S2c).

The above biogeographic classifications correspond to very general trends in environmental harshness. For species that are particularly sensitive to moisture deficits, such as the majority of Collembola, regions receiving a high amount of rainfall will on average be less harsh. For species that are not able to increase their body temperature above that of the immediate environment, such as again Collembola, regions of high temperatures will on average be less harsh. In that sense, the Inter-Tropical Convergence Zone, with a reasonably warm (cloudy) and moist climate, will be favorable to most sensitive species. Besides coldness and aridity, acid and metal-contaminated soils were also considered as harsh

habitats. Indeed, most tropical soils are acid, at least they exhibit pH values less than 5. However, if we except areas degraded by human activities in the tropics (pasture, mining,…), tropical rain forests are not characterized by nutrient shortage, due to (i) high organic inputs from the overstory, (ii) a high rate of mineral weathering in the soil. Tropical soils are fragile but not poor in nutrients, at least in the top few centimeters where most soil animals (*Willemia* included) are living (see Dos Santos Neves *et al.*, 2010; Brookshire *et al.*, 2012). Obviously, tropical areas also include harsher environments (which have been coded as such in our database), more especially in mountains above 3000 m (the Andes), white sands and seashores. As explained in the Introduction, during much of the geological past, environments might have been on average harsher on Laurasia rather than on Gondwana paleocontinents (Vršanský, 2005; Crisp *et al.*, 2010), among others reflecting the larger surface of landmasses of northern than of southern temperate regions which may lead to more climatic and thereby edaphic extremes in Laurasia and descendant land masses (except for Antarctica) (Chown *et al.*, 2004).

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Appendix 3 – Table. Biogeographic provenance of *Willemia* species. Biogeographic provinces according to Christiansen & Bellinger (1995). Gondwana-inherited provinc
type, Eurasia-inherited provinces in italic type, non-defined (Macaronesia and Central America) in normal type. Species belonging to both old continents were classified a
Columns corresponding to tropical provinces are shaded

	1	*2a*	*2b*	*3a*	**3b**	*4*	*5*	6	*7a*	*7b*	*8*	**10**	**14**	**15**	**17**	**18**	**19**	**20**	**21**	24a	**24b**	**25**	**27**	**28**	**29**	**36**	**Gondwana**	**Laurasia**	**Non-defined**
multilobata	√		√				√	√			√																√	
bellingeri																				√								√
trilobata													√													√		
namibiae													√													√		
similis	√								√	√	√									√							√	
christianseni									√																		√	
anophthalma	√	√	√		√	√	√		√		√													√				√
dubia									√		√																√	
scandinavica	√	√					√																				√	
koreana				√																							√	
iztaccihuatlensis																				√								√
bedosae							√																				√	
unispina		√																									√	
psammophila																				√								√
virae		√																									√	
tali							√																				√	
intermedia	√	√	√	√			√	√	√	√	√									√							√	
shanghaiensis				√																							√	
granulata	√										√																√	
fjellbergi	√																										√	
arida									√		√																√	
trisphaerae						√																					√	
elisabethum				√																							√	
denisi	√	√	√	√			√		√		√																√	
japonica				√																							√	
subbulbosa																				√	√					√		
persimilis											√									√				√				√
acantha																				√								√

bulbosa								√																					√			
meybholae																			√											√	
arenicola																			√											√	
nepalensis				√																					√						
neocaledonica													√			√									√						
nadchatrami													√	√											√						
brevispina								√					√		√			√		√		√	√		√	√					
annapurna				√																					√						
buddenbrocki	√			√		√	√					√	√					√						√						√	
wandae				√									√												√						
nosyboraha											√														√						
delamarei												√													√						
setonychia												√													√						
deharvengi													√			√									√						

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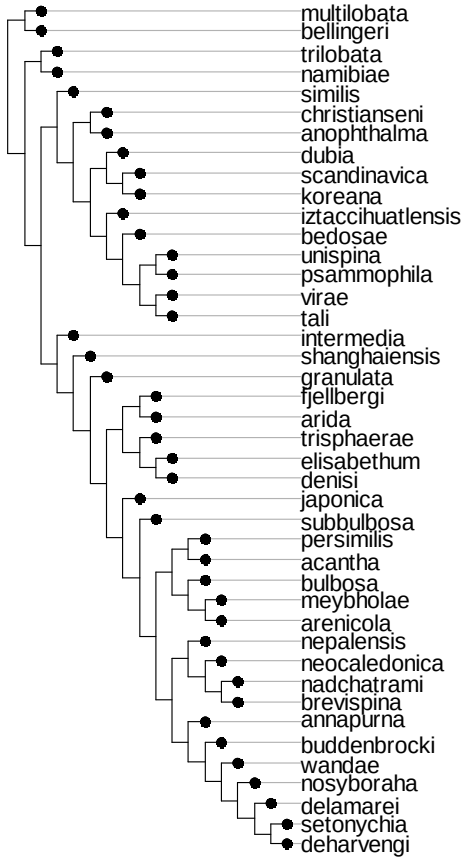
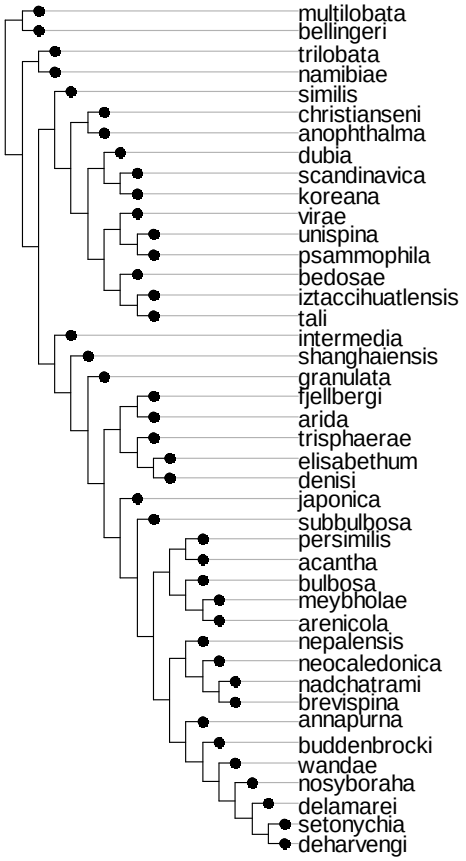
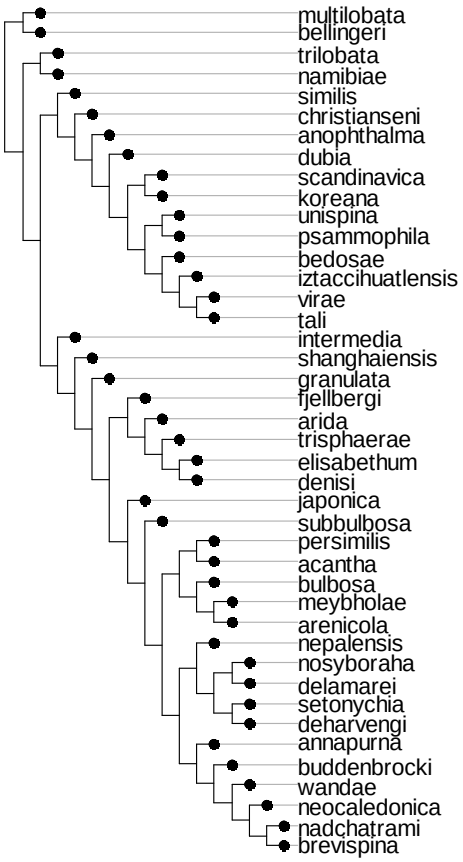
Appendix S3. Robustness of the analysis to variation in underlying phylogenetic trees

We have performed again all analyses with the 6 most parsimonious trees. The 6 trees are given below.

According to all these analyses, the results obtained with the 6 most parsimonious trees are equivalent to those obtained with the resulting tree used in the main text.






multilobata
bellingeri
trilobata
namibiae
similis
christianseni
anophthalma
dubia
scandinavica
koreana
unispina
psammophila
bedosae
iztaccihuatlensis
virae
tali
intermedia
shanghaiensis
granulata
fjellbergi
arida
trisphaerae
elisabethum
denisi
japonica
subbulbosa
persimilis
acantha
bulbosa
meybholae
arenicola
nepalensis
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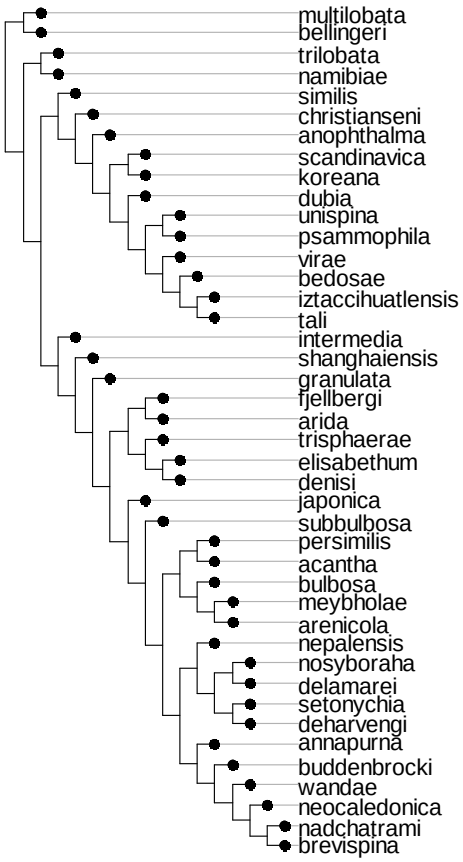
wandae
neocaledonica
nadchatrami
brevispina


multilobata
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scandinavica
koreana
dubia
unispina
psammophila
virae
bedosae
iztaccihuatlensis
tali
intermedia
shanghaiensis
granulata
fjellbergi
arida
trisphaerae
elisabethum
denisi
japonica
subbulbosa
persimilis
acantha
bulbosa
meybholae
arenicola
nepalensis
nosyboraha
delamarei
setonychia
deharvengi
annapurna
buddenbrocki
wandae
neocaledonica
nadchatrami
brevispina

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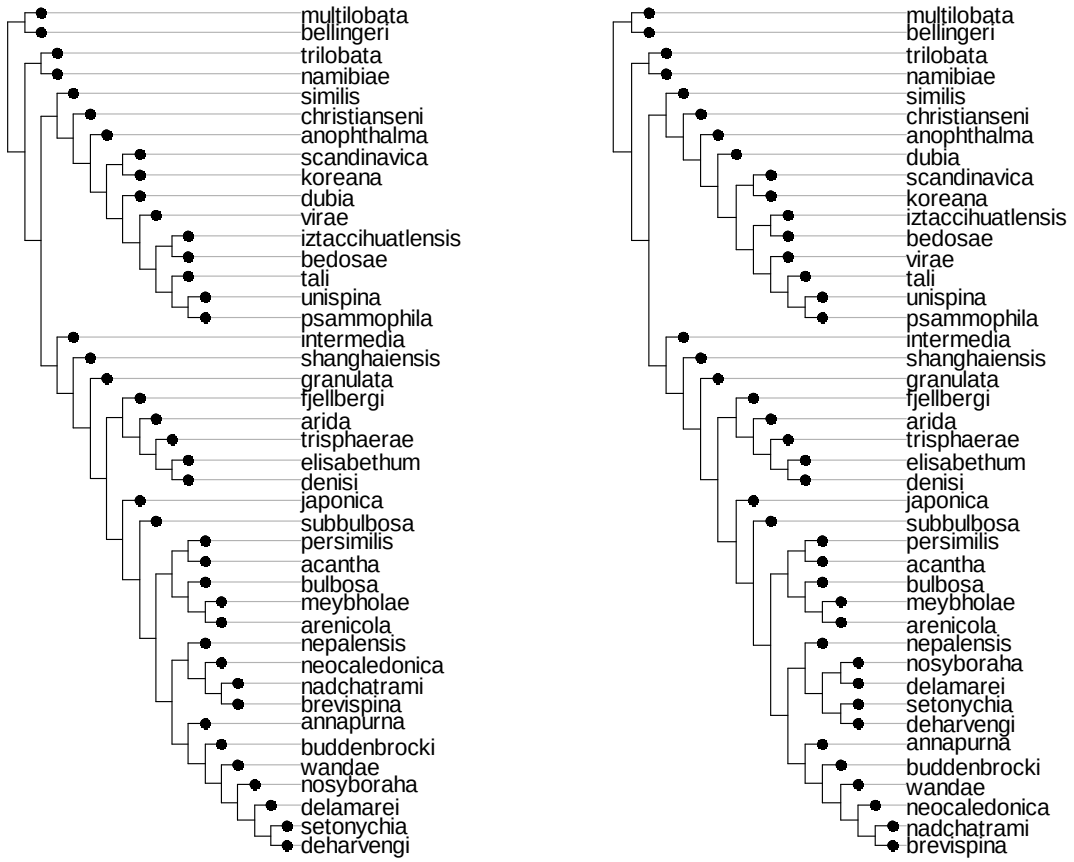


Phylogenetic conservatism in the use of harsh habitats

With all phylogenetic trees, the types of harshness under which species were found exhibited clear phylogenetic conservatism (root-skewness test P values varied from 0.001 to 0.003 for a statistic varying from 0.616 to 0.647, 1 meaning that the whole trait variation is at the root node). Also the number of types of harsh habitats used by a species was phylogenetically conserved (root-skewness test P values varied from 0.013 to 0.043, for a statistic varying from 0.623 to 0.660). When salinity was excluded from the array of harsh habitats a stronger conservatism was registered (root-skewness test P values varied from 0.001 to 0.019, for a statistic varying from 0.659 to 0.699). The presence/absence of *Willemia* species in harsh habitats (instead of their number used) exhibited an even clearer phylogenetic conservatism

when salinity was excluded from the array of harsh habitat (root-skewness test with all P values equal to 0.001, for a statistic varying from 0.754 to 0.786).

Uses of most types of harsh habitats are positively correlated

Phylogenetic principal components analysis (pPCA) showed strong positive correlations between all types of harsh habitats, with the exception of salinity. Use of all other types of harsh habitats scored distinctly positively on the same Principal Component (Fig. 1).

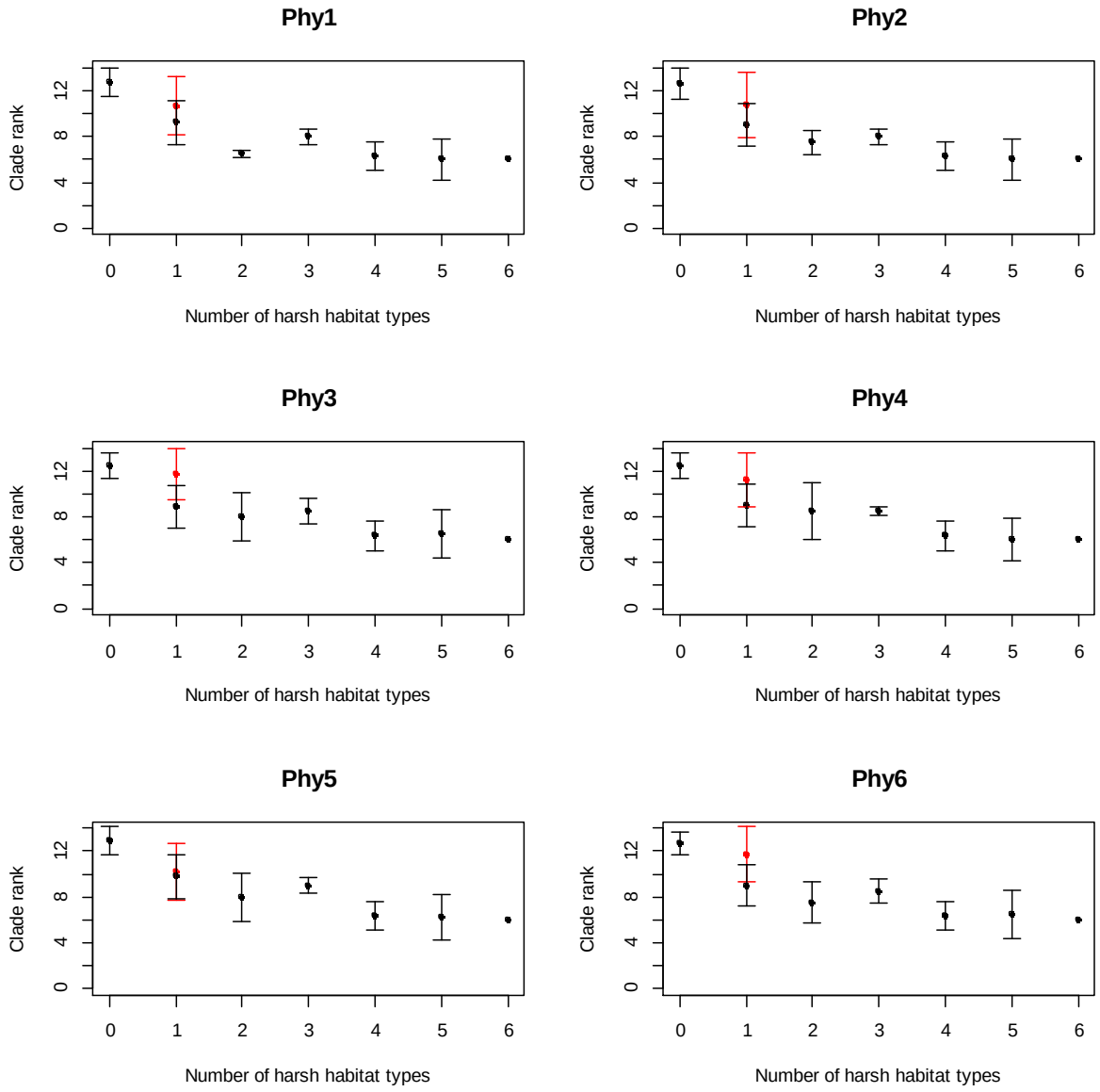
Appendix S3 Table. Ordination of correlations between uses of different types of harsh habitats, analysed by pPCA analysis (multivariate analysis based on phylogenetic distances). The table gives coordinates of harsh habitat types along the first principal component for the 6 dichotomous phylogenies provided above. Note that except for salinity, uses of habitats of all types of harshness are positively correlated.

	Phy1	Phy2	Phy3	Phy4	Phy5	Phy6
Xeric	-.343	-.398	-.396	-.414	-.426	-.395
Hydric	-.183	-.177	-.190	-.176	-.181	-.188
Arctic	-.389	-.395	-.380	-.420	-.398	-.373
Alpine	-.482	-.453	-.461	-.432	-.450	-.470
Acid	-.581	-.559	-.566	-.548	-.552	-.567
Metallic	-.201	-.198	-.197	-.202	-.190	-.195
Saline	.296	.312	.303	.305	.291	.299

Species using harsh habitats have lower clade ranks but are as numerous as species using mesic habitats

We found that the clade rank of species decreased with species' harshness breadth (PGLS; df=40, P values varied from 0.002 to 0.003 depending on the dichotomous phylogeny used). When salinity was excluded it appeared that the distance to the root of the phylogenetic tree was quite similar for all species using harsh habitats, independent of the number of harsh

habitat types they were using, all of the harshness-tolerant species being placed in a basal position (Appendix S4 Figure).



Appendix S3 Figure. Clade ranks, i.e. nodal distances to the root, of species using different numbers of harsh habitat types. Error bar = S.E. Note that species that do not use any harsh habitat are at a higher distance from the root (see text for analyses). This analysis has been done for each dichotomous phylogenetic tree given above. Species having a single harsh habitat type have been separated into those affected by salinity (red) and those affected by another harsh habitat type (black).

Geographical distributions: Species using harsh habitats tend to be Laurasian, and as a statistical consequence Laurasians tend to have low clade ranks

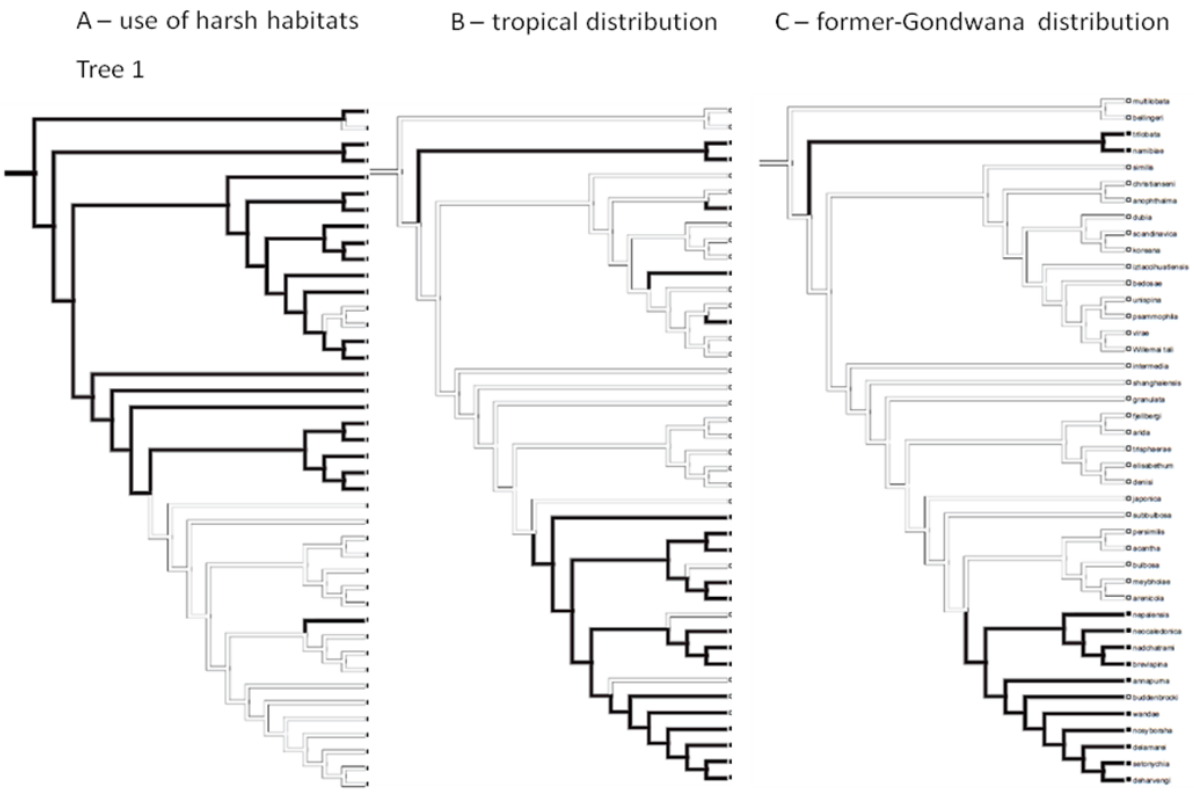
We found that species using harsh and mesic habitats were distributed differently across the globe. Species using harsh habitats tended to occur in present non-tropical regions, albeit the relationship was relatively weak (PGLS; df = 30; P values varying from 0.0004 to 0.0553). At the same time, species using harsh habitats were strongly restricted to former Laurasia regions (PGLS; df = 30; P values varying from 0.0002 to 0.0103).

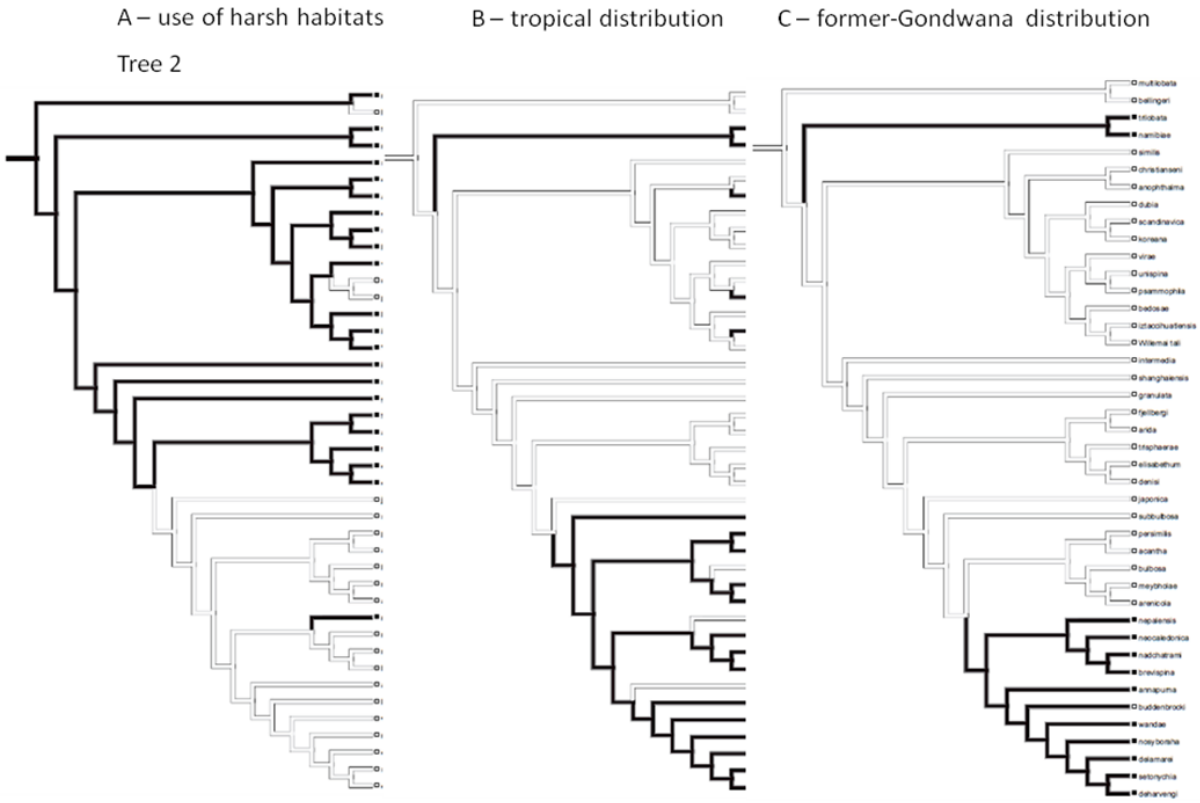
Low clade-rank species were strongly restricted to present non-tropical regions (n = 31 in all tests of this paragraph, tests based on phylogenetic permutations, all P values equal 0.001 whatever the dichotomous phylogenetic tree used). This relationship was maintained when including harshness breadth as a co-variable: harshness breadth and presence in present-day tropical regions were both related to low clade rank (P values were equal to 0.001 for harshness breadth, and they varied from 0.001 to 0.009 for presence in present-day tropical regions depending on the phylogenetic tree used; conclusions were not impacted by the order in which the two explanatory variables were entered in the model: changing the order gave P varying from 0.034 to 0.051 for harshness breadth, and equal 0.001 for presence in present-day tropical regions). Therefore the high harshness-tolerance of non-tropical species did not explain their low clade rank. Species of low clade rank also tended to be restricted to former Laurasia regions (P varied from 0.005 to 0.013 depending on the phylogenetic tree used). When including first occurrence in former Laurasia and second harshness breadth, both variables were significant (P varied from 0.002 to 0.004 for occurrence in former Laurasia, and from 0.007 to 0.017 for harshness breadth). But this relationship disappeared when including first harshness breadth in the model: occurrence in former Laurasia was not significant (P varying 0.239 from to 0.294) while harshness breadth was significantly related

to low clade rank (P varying from 0.001 to 0.002). Overall, this indicated that species using harsh environments are particularly bound to former Laurasia continents (above paragraph) and that - as a statistical consequence - we find many species of low clade rank on former Laurasia continents.

Reconstructions of ancestral states

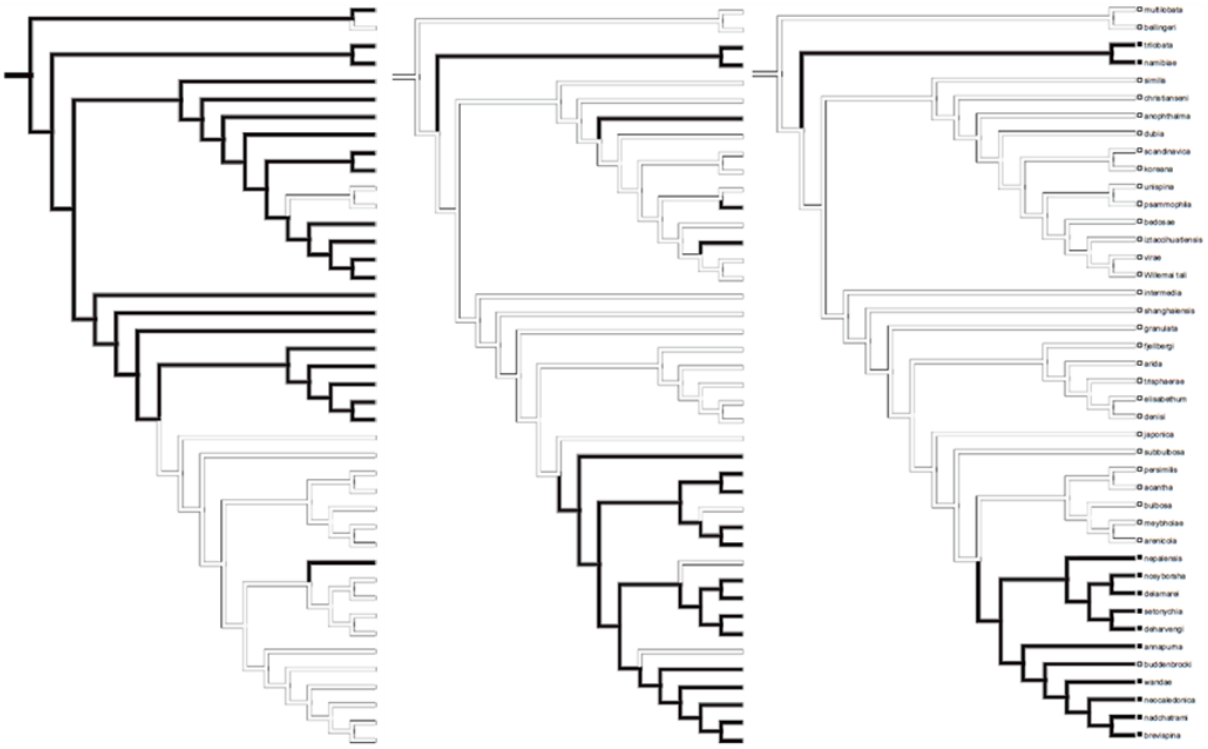
The below graphs show the reconstructions of the three traits analysed for each of the six trees. Visiul inspection shows that the different trees lead to the same conclusions on which trait states are ancestral and when they have changed throughout evolution.





A – use of harsh habitats B – tropical distribution C – former-Gondwana distribution

Tree 3



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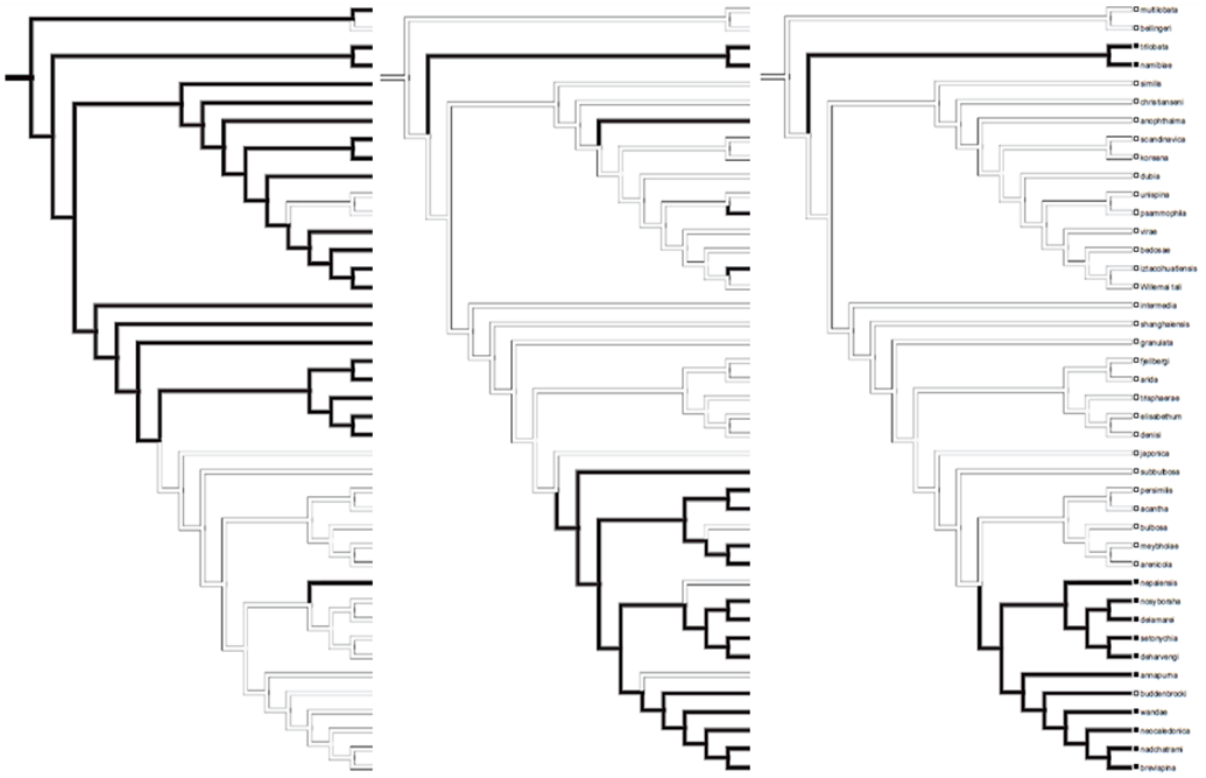
A – use of harsh habitats B – tropical distribution C – former-Gondwana distribution

Tree 4



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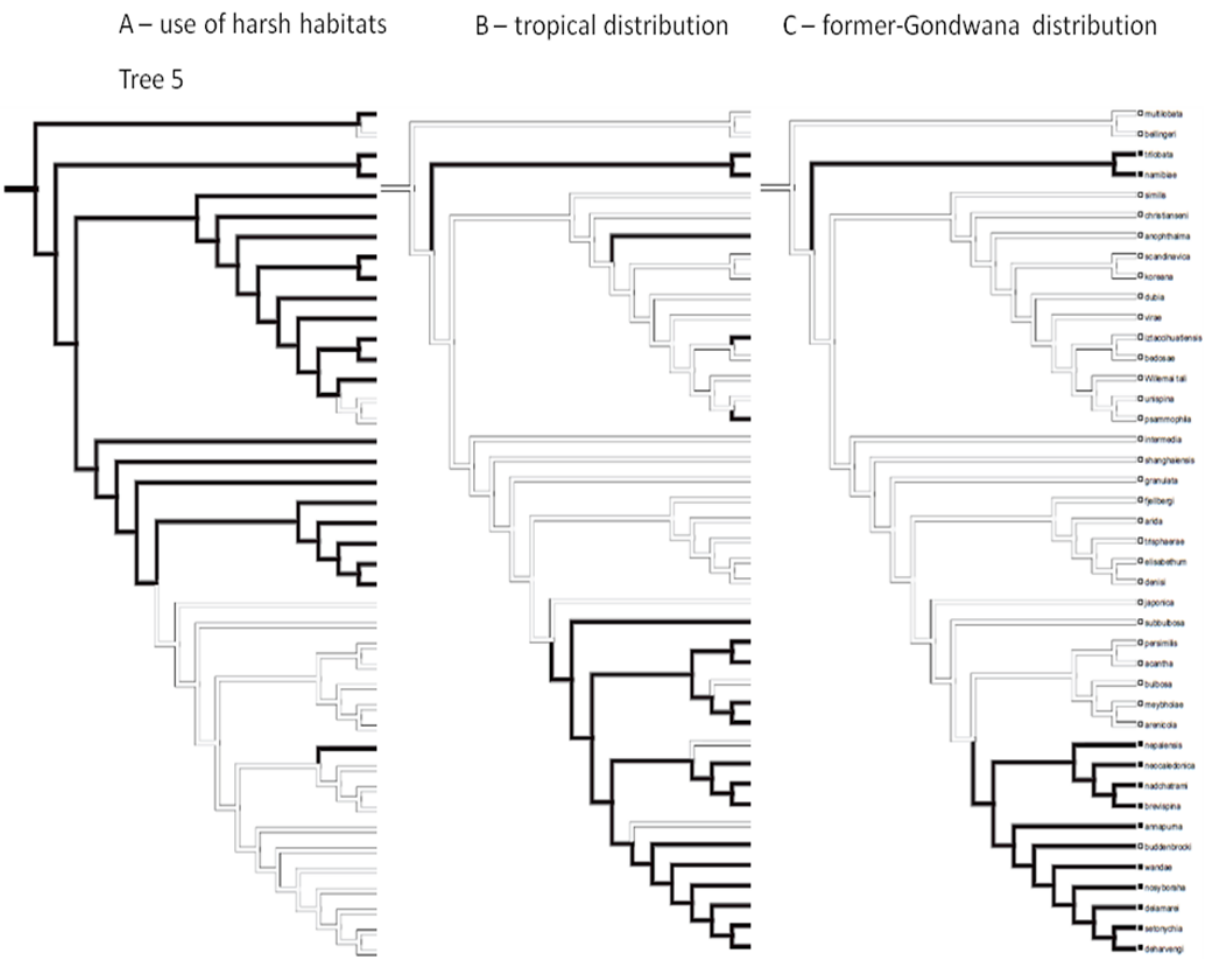

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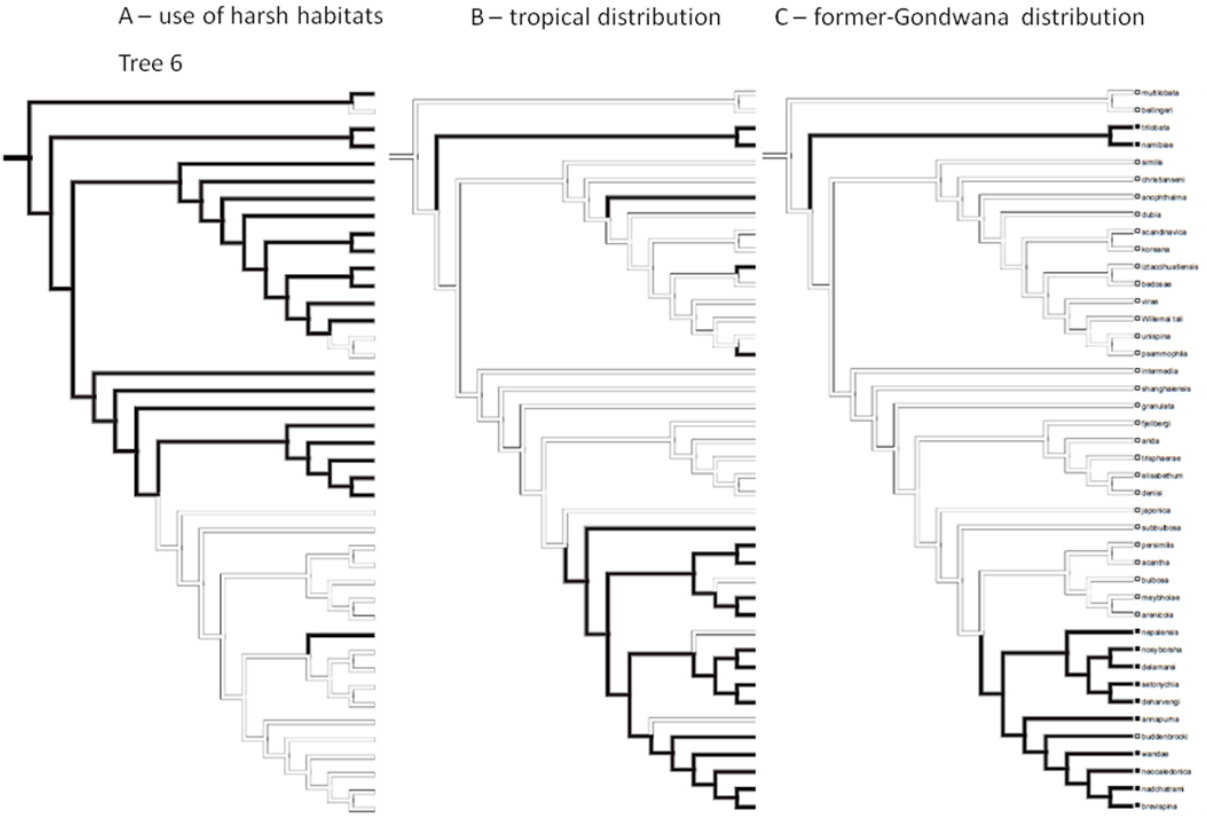

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